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Enchytraeids

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I. INTRODUCTION

Enchytraeidae (potworms) are a globally distributed family of small terrestrial and aquatic worms from the phylum Annelida, class Oligochaeta. Their size and generally whitish appearance distinguish them from their larger relatives, the earthworms (Chapter 6). Most species are between 2 and 20 mm long, although some species may reach up to 50 mm. With a body diameter of 0.05 to 1.5 mm enchytraeids belong to the soil mesofauna. Figure 1 shows the internal organization of enchytraeid worms. About 600 species of enchytraeids have been described, but this number is expanding steadily. This is a corollary partly to the relative late start of enchytraeid taxonomy, partly to the lack of sufficiently clear taxonomic criteria. Thus, much of the ecological research on potworms has been conducted on the family level. Like all oligochaetes, enchytraeids are hermaphroditic and most species reproduce sexually, although parthenogenetically (e.g., several species from the genera *Lumbricillus* and *Enchytraeus*) as well as asexually (e.g., *Enchytraeus fragmentosus*, *Buchholzia appendiculata*, and *Cognettia sphagnetorum*) reproducing species are also known. Combinations

of reproductive strategies may also occur. Terrestrial enchytraeids occur in almost all soil types, in divergent abundances, although their abundances may be characteristic for specific habitats. Average abundances range from several hundreds per square meter (m^{-2}) (in dry sclerophyll forests) to approximately 150,000 m^{-2} (in temperature and subalpine forests and moors) (Didden, 1993), but peak abundances may be much higher. Their populations exhibit clear seasonal dynamics, with maxima in late spring and autumn and minima in summer and winter in temperate zones, but in other climatic zones there may occur only one maximum and minimum (O'Connor, 1967; Dash, 1990). Table 1 lists some characteristic abundances reported from arable land, grassland and forest. Table 2 mentions some of the 50–100 species that are common in Middle European agricultural soils.

Like most other soil organisms and especially soil fauna, potworms have been ignored for a long time, in both natural and agricultural systems, because they were simply deemed unimportant. One of the first occasions when enchytraeids attracted scientific attention was when they were suspected to be potential pest organisms (Harker, 1889; Stoklasa, 1897; Gordon Hewitt, 1908). However, ecological research on potworms was also hampered by some practical problems: difficulties with their extraction from soil, and especially a lack of unambiguous taxonomic identification criteria. Since the development of relatively simple and reliable extraction methods (Nielsen, 1953; O'Connor, 1955) and a revision of enchytraeid taxonomy (Nielsen and Christensen, 1959, 1961, 1963), an increasing number of ecological studies have been carried out, and it has repeatedly been demonstrated that enchytraeids may constitute a major element of the soil faunal community in a variety of habitats.

II. BASIC REQUIREMENTS OF ENCHYTRAEIDAE

A. Soil Moisture

Because no histological protection structures against evaporation are known in enchytraeids, it is often assumed that they are susceptible to drought and therefore confined to moist habitats such as moors and swamps (e.g., Nielsen, 1995a; O'Connor, 1967, 1971; Dash, 1983, 1990). Although large numbers and biomasses are reported from wet places and a number of species even are restricted to aquatic or very wet terrestrial habitats, enchytraeid species may be able to tolerate extreme moisture conditions and substantial populations may occur in habitats where droughts occur (e.g., Yeates, 1967, 1968; Willard, 1974; Healy, 1980a,b). This may be explained by migration to moist microhabitats (Shindô, 1929; Peachey, 1963; Springett et al., 1970) or by ecophysiological adaptations (e.g., Drawert, 1968; Lasserre, 1975).
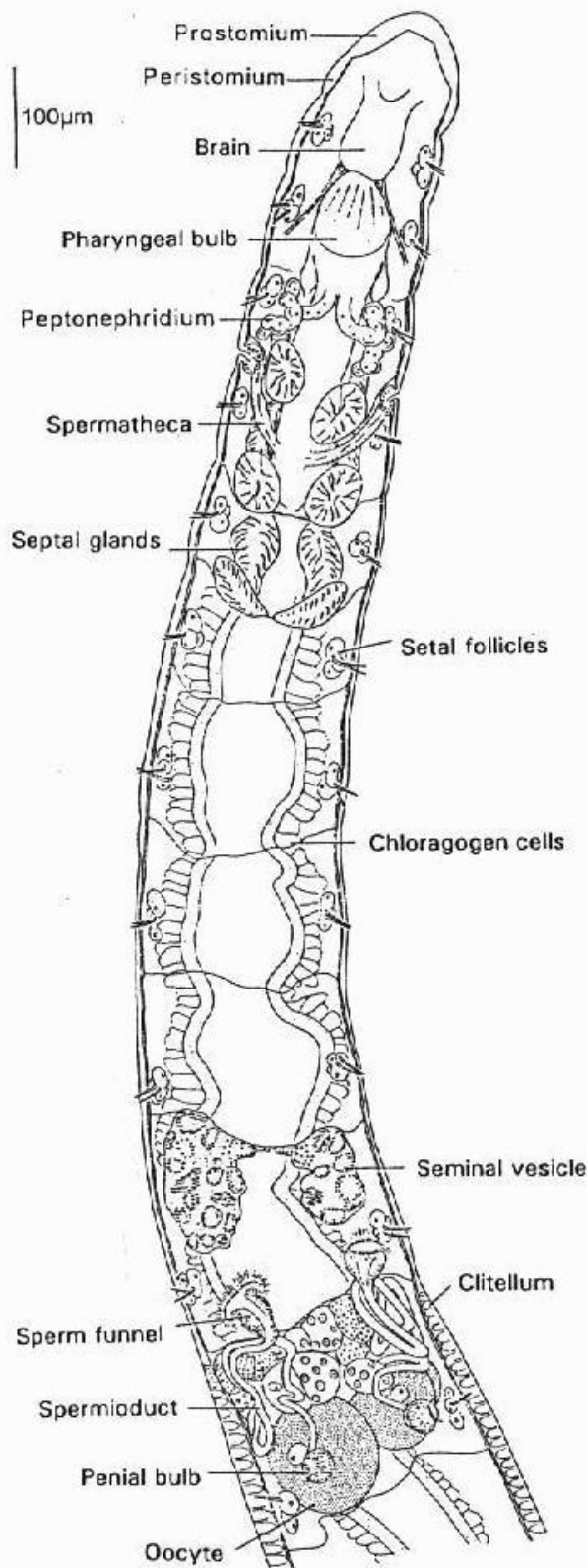
Figure 1. Internal organization of an enchytraeid worm (*Enchytraeus crypticus*), showing the anterior part of the body with taxonomically important criteria. After Westheide and Graefe, 1992.

Table 1. Average Abundance of Enchytraeidae in Arable Land, Grassland, and Forest, Based on Year-Round Sample Programs

Biotope	Country	Abundance (Number $\cdot$ m^{-2})	Author(s)
Arable land			
Rye	Poland	9,800	Ryl, 1977
Potato	Poland	13,000	
Lucerne	Poland	5,700	
Sugar beet	Poland	9,600	
Sugar beet	Netherlands	30,000	Didden, 1991
Winter wheat	Netherlands	12,000	
Wheat	Canada	4,650	Willard, 1974a
Barley	Sweden	8,100	Lagerlöf et al., 1989
Rice/wheat/barley	Japan	2,200	Nakamura, 1987
Grassland			
Tropical	India	3,800	Thambi & Dash, 1973
Natural	Canada	30,000	Willard, 1974a
Irrigated	Canada	39,000	
Unused hay land	Germany	49,000	Brockmann, 1984
Abandoned field	Sweden	23,800	Persson & Lohm, 1977
Grazed, 10 sheep ha^{-1}	Australia	6,000	King & Hutchinson, 1976
Grazed, 20 sheep ha^{-1}	Australia	2,600	
Grazed, 30 sheep ha^{-1}	Australia	2,300	
Grazed	Japan	1,650	Nakamura, 1980
Grazed	Japan	1,400	
Cut, fertilized	Japan	2,800	
Ley	Sweden	5,500	Lagerlöf et al., 1989
Meadow	Poland	17,000	Ryl, 1977
Ryegrass-clover sward	New Zealand	13,800	McColl, 1984
Forest			
Deciduous	Germany	143,000	Heck & Römbke, 1990
Deciduous, beech	USA	6,400	Blair et al., 1994
Deciduous, oak	Hungary	18,000	Dózsa-Farkas, 1973b
Deciduous, ash-alder	Poland	29,500	Makulec, 1983
Deciduous, oak-hornbeam	Poland	38,600	
Mixed, pine-oak	Poland	39,500	
Mixed, pine-oak	Germany	42,000	Heck & Römbke, 1990
Coniferous, pine	Germany	134,000	Ellenberg et al., 1986
Coniferous, pine	USA	25,200	Blair et al., 1994
Coniferous, douglas fir	Canada	5,700	Marshall, 1974
Coniferous, subalpine	Japan	138,000	Kitazawa, 1977
Coniferous, subalpine	Japan	10,000	Kitazawa, 1971
Subtropical rainforest	Japan	10,000	
Tropical rainforest	Malaysia	8,900	Chiba et al., 1976; Kira, 1976

Sample depths varying, but assumed sufficient to yield the major part of the populations.

Table 2. Common Enchytraeid Species in Middle European Agricultural Soils

Genus	Species	General Information
Enchytraeus	*E. bulbosus* *E. buchholzi agg.* *E. lacteus* *E. minutus agg.* —	*Enchytraeus* species are favored by accumulation of nitrogen-rich organic material and show high fluctuations of population sizes according to the availability of food.
Fridericia	*F. bisetosa* *F. bulboides* *F. galba* *F. parionana* *F. perrieri* —	The numerous *Fridericia* species are soil dwellers that take up soil substrate while feeding. With body lengths up to and exceeding 20 mm they belong to the large Enchytraeidae. Preferring soils with pH around 5–7, they are also characteristic elements of mull-humus forest soils.
Enchytronia	*E. annulata* *E. parva* *E. minor*	The genus *Enchytronia* consists of small species that may be classified as true soil dwellers.
Henlea	*H. perpusilla* *H. ventriculosa*	*Henlea* species are predominantly found in meadows and grassland. Very high dominances have been found in trundra soils.
Achaeta	*A. pannonica* —	The genus *Achaeta* contains acid-tolerant forest species as well as neutrophilic species which are frequently encountered in agricultural soils. *A. pannonica* is highly abundant in continental agrocenoses and is typical of sandy soils and favorable climatic conditions.

In agroecosystems the moisture regime may be an important determinant of enchytraeid population dynamics, but in more natural habitats enchytraeid communities are likely to be affected by a combination of moisture regime and factors such as the species composition, temperature conditions, organic matter content and structure of the soil, and interactions with soil flora and other soil fauna.

B. Temperature

In cultures of species from the genera *Enchytraeus* and *Lumbricillus* optimum temperatures for reproduction have been found to range form 8°C to 28°C (Trappmann, 1952; Ivleva, 1969; Learner, 1972; Didden, 1991). As temperature limits for reproduction in *Enchytraeus buchholzi*, Trappmann (1952) reported a lower limit of 0.5°C and an upper limit of 37°C. The response to field temperature regimes is likely to be species-dependent. Klungland (1981) reported a sharp reduction in numbers of *Henlea perpusilla* after the air temperature had fallen below zero, but numbers of *Bryodrilus ehlersi* remained unaffected. Dózsa-Farkas (1973a) showed that *Stercutus niveus* is able to survive periods of frost, while *Fridericia* species retreat to deeper soil layers to survive. Some species are adapted to very low temperatures, such as the Alaskan "ice worm," *Mesenchytraeus solifugus*, which lives in the snow cover of glaciers (Goodman and Parris, 1971). Thus, temperature regimes are unlikely to inhibit the establishment of enchytraeid populations. Under field conditions temperature may influence species composition and population density, rather than presence or absence of potworms, and act predominantly in combination with soil moisture.

C. pH

Although large enchytraeid populations may be found in neutral to acid habitats, substantial populations have also been reported from more alkaline sites (e.g., Yeates, 1967, 1968; Healey, 1980a). Healy and Bolger (1984) mentioned pH as one of the most important environmental factors for the distribution of enchytraeid species in Irish wetlands. In these wetlands, there occurred fewer species in acid (pH < 5) than in neutral to alkaline sites. Standen (1984) found a negative correlation between the abundance of potworms and soil pH. This was mainly caused by the reaction of *Cognettia sphagnetorum* and to a lesser extent of *Achaeta affinis*, *Achaeta eiseni*, and *Cognettia glandulosa*, while the abundances of other species were not, or were slightly positively, correlated with soil pH. Moreover, diversity of the enchytraeid communities was positively related to soil pH. Again, Graefe (1989, 1990) reported a decline of enchytraeid numbers in response to liming in German beech and fir forests, but a concurrent increase in species number, diversity, and evenness with treatments up to 5000 kg $CaCO_3$ ha^{-1}. In experimental agricultural sites in Scotland, Dawod and FitzPatrick (1993) found a similar response of enchytraeids to soil pH: here *Marionina argentea* dominated at pH 4.5.

   In several other field experiments in which the pH of coniferous forest plots was manipulated by acidification, liming, or fertilization (e.g., Lohm et al., 1977; Abrahamsen et al., 1980; Huhta et al., 1983; Persson et al., 1987; Heck and

Römbke, 1990), it was found that *Cognettia sphanetorum* reacted positively to slight acidification, sometimes after a temporary reduction in population size, and negatively to liming. Reaction of lumbricids, in these cases *Dendrobaena octaedra*, was the reverse (see Section III.A.1.). Abrahamsen et al. (1980) reported that *Mesenchytraeus pelicensis* showed a similar reaction to that of *Cognettia sphagnetorum*, whereas *Enchytronia parva* increased with liming. From a short-term experiment with *Cognettia sphagnetorum* Heungens (1984) concluded that the effect of changes in pH was insignificant compared to the effect of changes in the electrical conductivity of the soil solution. This might be an alternative explanation for the shock effect observed in various field experiments after pH manipulations or fertilizer applications.

Thus, it may be concluded that the dominance of enchytraeids in acid habitats results because some species, notably *Cognettia sphagnetorum* and several *Achaeta* species, are acidophilic or acid-tolerant and possibly also because of the absence of competitors. Most other enchytraeid species, however, occur in only slightly acid to alkaline habitats.

D. Soil Texture

Soil texture may be an important factor determining species composition, but not total enchytraeid abundance. Clayey soils are characterized by a dominant occurrence of *Fridericia* species, while *Enchytronia* species and some *Achaeta* species prevail in sandy soils. Fründ et al. (1992) found higher enchytraeid abundances in sandy arable soils than in similarly managed fields on loam, but species diversity was the same. Decrease in competition that resulted from the presence of fewer earthworms (see Section III.A.1) in the sandy soils was suggested to account for these findings.

E. Food

Gelder (1984) studied the feeding behavior of the littoral species *Lumbricillus lineatus* and found that this species ingests mineral particles and organic debris with diameters less than 60 µm, an upper limit which is probably determined by the maximum mouth opening. Small particles can be sucked up directly, but ingestion mostly occurs by protracting the pharyngeal pad, the surface of which is covered with adhesive secretions from the septal glands (see Fig. 1). The food mass is transported from the pharynx to the intestine by peristaltic movements and ciliary action. In terrestrial enchytraeids the pharyngeal pad probably fulfills the same function in the ingestion of food. To assess the impact of enchytraeid feeding on the functioning of ecosystems, the question must be resolved whether enchytraeids should be classified as primary or as secondary

decomposers, i.e., whether they are saprovores or microbivores (see Chapter 1, Figure 3). Dougherty and Solberg (1961) succeeded in culturing *Enchytraeus fragmentosus* axenically on a medium containing lamb liver extract. From this, it may be concluded that this species is not an obligatory microbivore and may be capable of obtaining food from sources like dead organic material and root exudates. Palka and Spaul (1970) found in *Lumbricillus rivalis* (as identified by Learner, 1972) the capability of digesting carbohydrates, fats, and proteins. These data seem to indicate that enchytraeid species are saprovorous. There are, however, also strong indications that microorganisms play a substantial role in the feeding biological characteristics of potworms. Dash and Cragg (1972) and Dash et al. (1980) reported that several enchytraeid species feed on fungi; Hedlund and Augustsson (1995) demonstrated grazing of *Cognettia sphagnetorum* on the fungus *Morteriella isabellina* in a laboratory experiment, and Brockmeyer et al. (1990), using labeled methionine, demonstrated that *Enchytraeus cf. globuliferus* and *Enchytraeus minutus* digested microorganisms, and that significantly less fresh plant material was assimilated. Studies of the gut contents of *Fridericia striata* (Toutain et al., 1982) and *Cognettia sphagnetorum* (Ponge, 1991) revealed that ingested structural plant material underwent little change, but that microorganisms and cytoplasm of plants and fungi were digested during passage through the gut. Obviously, enchytraeids are capable of utilizing easily degradable organic compounds produced by plants or microorganisms, but competition with the microbial community for these compounds may restrict their availability. As the feeding biological features of only few species have been studied so far, species-related differences in feeding activities remain to be investigated.

   In production-ecological studies enchytraeids are often treated as being 50% saprovorous, 25% bacterivorous, and 25% fungivorous (Persson et al., 1980; Lagerlöf et al., 1989). From the studies cited previously, however, it appears that microbivory may be underestimated in this way. In our view, the assumption of Whitfield (1977) that enchytraeids are 80% microbivorous and 20% saprovorous may be more realistic.

F. Spatial Distribution

Generally enchytraeids are distributed contagiously, occurring in more or less randomly distributed clusters of 100–1000 cm² that may show appreciable species-dependent and temporal differences (Didden, 1993). Such clusters probably are formed in response to heterogeneity and changes in biotic and abiotic parameters of the habitat. Some studies (Head, 1967; Heungens, 1968; Way and Scopes, 1968; Didden, 1991) established an association of potworms with the

rhizosphere, suggesting a connection with root exudates or decaying roots, either directly or through the activity of microorganisms.

Vertical distribution of enchytraeids probably is often related to the distribution of organic material on the one hand, and to physical factors on the other. In undisturbed habitats populations are mostly concentrated in the upper layers of the soil profile, coinciding with the location of the bulk of organic material and decomposition processes. In ploughed agricultural fields a large part of the populations can be found at the ploughing depth, probably in response to the inverted distribution of the organic material (Lagerlöf et al., 1989; Didden, 1991). Vertical migration in potworms may also be induced by physical factors such as soil moisture and temperature (e.g., Shindô, 1929; Peachey, 1963; Springett et al., 1970; Ellenberg et al., 1986). Especially in extreme situations like drought or frost, however, it will always be questionable what proportion of the actual vertical distribution may be attributed to differential mortality (O'Connor, 1957) and what part to vertical migration.

Although the distribution of organic material and physical factors undoubtedly are important determinants, it has repeatedly been shown that the vertical distribution of potworms is also species-dependent. In Scots pine stands, for instance, Gröngröft and Miehlich (1983) and Graefe and Fründ (1993) found *Cognettia sphagnetorum* mainly living in the litter layer, *Achaeta brevivasa* occupying the deeper layer, and *Marionina clavata* taking an intermediate position. MacLean (1980) reported seasonal as well as species-dependent vertical distributions for *Cernosvitoviella atrata, Henlea perpusilla,* and a *Mesenchytraeus* species in an Alaskan tundra site. Again, from a Hungarian hornbeam–oak forest Dózsa-Farkas (1991) described *Fridericia profundicola,* a species that only occurred from 40 cm depth downward.

III. ECOLOGICAL IMPORTANCE

A. Interrelations with Other Soil Organisms

1. Competition

Little is known about competitive interactions between enchytraeids and other soil organisms. Competition for food may occur between enchytraeids and microarthropods, since their diets may partly overlap (see also Chapter 7). Way and Scopes (1968) found a significant increase in enchytraeid numbers after application of insecticides to agricultural plots and the resulting strong reduction of microarthropod numbers. According to Alejnikova et al. (1975) and Lagerlöf and Andrén (1985), who studied decomposition in manure and barley straw, respectively, potworms appear to participate mainly in the early stages of decomposition

and are followed by microarthropods. Besides competition, differences in food preferences and other requirements may also play a role here.

Several authors have suggested an antagonistic relationship between enchytraeids and earthworms. Nielsen (1955b) reported that the abundances of both groups were negatively correlated and assumed the ecological status of both groups to be completely different. This view is in some degree corroborated by Górny (1984), who in Dutch polder soil found fewer potworms in plots inoculated with earthworms than in control plots. Yet, the differences were mainly caused by one enchytraeid species, *Henlea ventriculosa*, suggesting the antagonistic effect to be interspecific rather than to exist between the two groups. In an experiment where the earthworm *Eisenia fetida* and *Enchytraeus albidus* were cultured together Haukka (1987) observed increased mortality of *Eisenia fetida*, and impeded growth at 25°C but faster growth at 15°C as compared to that in cultures with *Eisenia fetida* alone. However, both species showed optimal populations development at different temperatures and moisture levels, suggesting that in natural environments they occupy different niches. Haimi and Boucelham (1991) conducted a laboratory experiment introducing *Lumbricus rubellus* in a simulated coniferous forest soil containing its natural fauna (including the enchytraeid *Cognettia sphagnetorum* and the earthworm *Dendrobaena octaedra*). They recorded fewer enchytraeids in the presence of *Lumbricus rubellus* than in its absence, while *Dendrobaena octaedra* remained unaffected. The results of another experiment, performed by Hyvönen et al. (1994), with *Cognettia sphagnetorum* and *Dendrobaena octaedra* suggest competition for food between these species, the outcome of which is determined by soil pH. Positive relations between earthworm and enchytraeid species have also been observed (Graefe, 1993a). Bhatti (1967) reported associations of enchytraeids with the earthworms *Bimastos parvus* and *Pheretima posthuma*, and with Collembola. Zachariae (1967) mentioned that potworms consumed the excrements of lumbricids, thereby exposing enclosed litter that could be consumed once more by earthworms. Thus, some species of Enchytraeidae may have the same requirements as earthworms, but are better adapted to extreme (notably acid or cold) situations and are not able to compete with earthworms under other ecological conditions (see also Chapter 6). The majority of enchytraeid species, however, may have more complex relations with earthworms, and thus occupy at least partly different niches. Thus far, no conclusive evidence has been presented for competition between enchytraeid species and other members of the soil fauna.

2. Predation

The abundance of Enchytraeidae and the apparent lack of protective mechanisms make them an obvious prey. Actually, few studies mention predators of

enchytraeids. In a review on predatory soil nematodes, Small (1987) listed a number of taxa (notably larger Dorylaimida and Mononchida) that were found to feed on potworms. Mostly, however, it was not clear whether live or dead enchytraeids were consumed. Direct observations of nematode predation on enchytraeids were reported in the species *Anatonchus amiciae* (Coomans and Lima, 1965), *Prionchulus punctatus* (Small, 1987), *Nygolaimus vulgaris* (Thorne, 1930), *Sectonema ventralis* (Thorne, 1930), and *Butlerius degrissei* (Grootaert et al., 1977). Singer and Kranz (1967) successfully used enchytraeids as a food for *Macrocheles superbus, Macrocheles robustulus*, and *Glyptholaspis confusa*, indicating that some mesostigmatid mites may prey on potworms, and Heungens (1969) suggested that *Parholaspulus alstoni* might be an important predator on enchytraeids in azalea cultures. Sergeeva (1987) performed serological analyses of the gut content of several predatory soil invertebrates, and found that especially the young larvae of the rhagionid flies *Ragio scolopaceus* and *Ragio tringarius* probably feed on enchytraeids. The adults of several species of carabid beetles, notably *Abax ater* and *Abax parallelus*, were reported to prey on oligochaetes (enchytraeids and lumbricids) (Loreau, 1983). Using an immunological technique (enzyme-linked immunosorbent assay [ELISA]), Poser (1991) quantitatively determined the prey consumption by the centipedes *Strigamia acuminata, Lithobius mutabilis*, and *Geophilus insculptus*. Both geophilomorphic species (*Strigamia acuminata* and *Geophilus insculptus*) favored enchytraeids and lumbricids as a food source (see Chapter 8), while *Lithobius mutabilis* preferred more mites and springtails. The centipede community consumed about 8% of the enchytraeid production.

3. Parasitism and Commensalism

Parasitic and commensal organisms associated with potworms have been recorded from various taxa, of which Protozoa (Chapter 3) are the most frequent occurring. Stout (1954) observed facultative parasitism on enchytraeids by the ciliate *Tetrahymena rostrata*, normally free-living in litter and soil, but Bamforth (1988) classified *Tetrahymena* species as being facultatively symbiotic. Gelder (1984) reported the occurrence of Sporozoa species in the alimentary canal of *Lumbricillus lineatus*. Purrini (1983, 1987) reported enchytraeids were frequently infected by microorganisms, especially in polluted areas, where infection rates could reach 70%. Pathogenic agents identified were viruslike organisms, bacteria, fungi, and protozoa. Infection could occur in various tissues, and frequently caused lethal diseases. Gregarinid protozoa were the most abundant organisms in potworms; these organisms were probably not parasitic, however, living as commensals in the gut lumen.

Apart from the work of Poser (1991), little is known about the impact of predation and parasitism on enchytraeid populations. Yet, the qualitative evidence, and notably the variety of predators and parasites reported, indicates that substantial losses might occur through these interactions, influencing enchytraeid population dynamics considerably.

B. Ecological Significance of Enchytraeid Associations

Together with other soil fauna species, enchytraeid species constitute characteristic associations that are determined by environmental conditions (Graefe, 1993a). Similar associations are formed by microorganisms. Jointly these associations form a functional complex: the decomposer community. Typical of decomposer communities is the extraordinarily large species diversity, which renders it practically impossible to identify all organisms involved. The use of indicator species nevertheless allows cenological characterization of this complex. For this, species groups (taxocenoses) that allow conclusions concerning the structure of the decomposer community as a whole are recorded. An appropriate classification, based on characteristic species from the annelid cenosis, was suggested by Graefe (1993a).

For a number of reasons the annelid cenosis is suitable for characterization both of decomposer communities and of environmental conditions. The assignment of particular species to various life forms allows a differentiated characterization of the community structure. As regards earthworms, the reader is referred to Chapter 6. With enchytraeids, life forms may be distinguished by the vertical distribution in the humus profile, food relations, and the reproductive strategy (Graefe, 1996). As with plants, species may be classified according to their ecological response to soil moisture and acidity. For these factors, the system of plant indicator values (Ellenberg, 1979) was adopted for annelids (Graefe, 1990, 1993a, 1993b). The sensitivity of enchytraeids is mainly based on the fact that, phylogenetically, they are still aquatic animals. In contrast to soil arthropods they are dependent on, and live in close contact with, the soil solution and share the same microenvironment as plant roots and microorganisms. In acid forest soils, toxic ion concentrations in the soil solution are indicated by sharp delimitation of vertical distribution of enchytraeids in the mineral soil, while a decomposer refuge has developed in the litter layer. In tests with natural seepage water it was demonstrated that the toxic effects on enchytraeids of the combined action of acids and free Al ions, dependent on the Ca/Al molar ratio, were similar to those on plant roots (Graefe, 1991). Thus, enchytraeid associations may profitably be used as an instrument for a detailed site characterization that may indicate environmental changes, or tendencies to change, for instance, in ecological

impact assessment or in soil monitoring programs (Cordsen, 1993; Fründ and Graefe, 1994; Beylich et al., 1995).

C. Role of Enchytraeids in Nutrient Cycling

Respiration data determined for several enchytraeid species indicate appreciable interspecific differences in the relation between body mass and respiration rate (Nielsen, 1961; O'Connor, 1963; Lasserre, 1971; Standen, 1973). Moreover, actual respiration under field conditions is likely to be higher (Standen, 1973; Wightman, 1977). Nevertheless, the experimentally obtained relationships between biomass and respiration rate have been used to construct widely applied common respiration equations for Enchytraeidae (e.g., Persson and Lohm, 1977; Phillipson et al., 1979).

Table 3 lists the mean biomass, estimated respiration and consumption, and proportion of total soil respiration accounted for by enchytraeids in arable, grassland, and forest sites. The direct contribution of enchytraeids to total soil respiration ranges from 0.3% to 5.2% (ca. 2% on average). Didden et al. (1994) estimated nitrogen mineralization by enchytraeids in Dutch winter wheat fields to amount to 0.8–1.6 N ha^{-1} yr^{-1} or 0.8%–2% of the total mineralization. As a result of enchytraeid population dynamics and the course of soil temperature maximum nitrogen mineralization by enchytraeids occurred during the later part of the growing season. This may entail enhanced chance of nitrogen losses by leaching during this period in cases where there is no nitrogen demand from the crop.

Indirect effects of potworms on decomposition processes may result from enchytraeid influence on the microbial community and its activity; via comminution of organic material, mixing of organic material with the soil, (selective) grazing on microorganisms, and dispersal of spores and cysts (e.g., Toutain et al., 1982; Ponge, 1984; Wolters, 1988) (see Chapters 3 and 10). Indirect effects may also result from selective immobilization or excretion of nutrients such as Ca^{++} (Anderson et al., 1983). Such effects are difficult to quantify, but might be important in any ecosystem with an appreciable population of enchytraeids. This is illustrated by calculating enchytraeid consumption from the data in Table 3, using a R/C ratio of 0.168 (Didden, 1991). It then appears that 2.4% to 31% of the organic matter input may pass through enchytraeid populations.

D. Impact of Enchytraeids on Soil Physical Properties

Among others, Zachariae (1964), Babel (1968), Thompson et al. (1990), and Dawod and FitzPatrick (1993) observed that mor or moder humus layers

Table 3. Average Biomass of Enchytraeidae, Estimated Respiration and Consumption, and Proportion of Total Soil Respiration Accounted for by Enchytraeids, in Arable Land, Grassland, and Forest.

Biotope	Country	Biomass (g dw · m^{-2})	Respiration (kJ · m^{-2} · yr^{-1})	Consumption (kJ · m^{-2} · yr^{-1})	Percentage of Total Soil Respiration	Author(s)
Arable land						
Barley	Sweden	0.59	109.3	651	1.5	Lagerlöf et al., 1989
Lucerne	Poland	0.17	54.4	324	—	
Rye	Poland	0.11	61.1	364	0.9	Ryl, 1980;
Sugar beet/wheat	Poland	0.51	77.9	464	—	Golebiowska et al., 1974
Potato	Poland	0.32	134.8	802	0.4	
Winter wheat	Netherlands	0.20	58.8	350	0.8	Didden, 1991
Sugar beet	Netherlands	0.55	241.2	1436	3.2	
Grassland						
Tropical	India	0.02	—	—	1.0	Dash et al., 1974
Grazed, 10 sheep ha^{-1}	Australia	0.12	143.0	851	1.1	Hutchinson & King, 1979
Grazed, 10 sheep ha^{-1}	Australia	0.10	110.1	655	1.9	Hutchinson & King, 1980
Grazed, 20 sheep ha^{-1}	Australia	0.05	62.4	371	1.0	
Grazed, 30 sheep ha^{-1}	Australia	0.04	44.0	262	1.8	
Grazed meadow	England	2.16	427.4	2544	2.0	Macfadyen, 1963
Hay meadow	England	1.76	—	—	—	Standen, 1984
Meadow	Poland	0.26	132.3	788	—	Ryl, 1980

Pasture, dry	Denmark	0.53	148.0	—	Nielsen, 1961
Pasture, mesic	Denmark	0.55	193.8	—	
Pasture wet	Denmark	1.89	651.8	—	
Ley	Sweden	0.34	56.3	0.5	Lagerlöf et al., 1989
Lucerne ley	Sweden	0.54	108.4	0.9	
Forest					
Deciduous	Germany	4.00	—	5.2	Heck & Römbke, 1990
Deciduous, beech	England	0.34	85.6	1.6	Phillipson et al., 1979
Deciduous, ash-alder	Poland	0.32	71.0	0.9	Makulec, 1983
Deciduous, oak-hornbeam	Poland	0.43	87.6	1.6	
Mixed, pine-oak	Poland	0.45	104.2	1.9	
Mixed, pine-oak	Germany	0.70	—	2.3	Heck & Römbke, 1990
Coniferous, pine	Germany	1.35	—	4.5	
Coniferous, pine	Sweden	0.46	103.2	0.9	Lundkvist, 1982
Coniferous, subalpine	Japan	1.17	383.4	1.6	Kitazawa, 1977
Subtropical rainforest	Japan	0.20	176.1	0.8	Kitazawa, 1971

Biomass figures originally presented as fresh weight converted to dry weight using fresh weight/dry weight ratios mentioned by the author (ranging from 5.0 [Standen, 1984] to 7.69 [Ryl, 1977, 1980]), or the value 5.56 (Edwards, 1967), where no fresh weight/dry weight ratio was mentioned. Proportions of total soil respiration accounted for by potworms were either taken from the publications or expressed as percentage of the energy content of the litter entering the soil (MacFadyen, 1963), if mentioned.

occasionally consist to a large extent of enchytraeid and microarthropod excrements. According to Toutain et al. (1983), enchytraeid excrements are very persistent and form particulate layers on leaves or needles. Jegen (1920) and Kubiena (1955) suggested that potworms may produce an extensive, be it spatially restricted, burrow system with a spongy appearance. Tunneling behavior of *Lumbricillus lineatus* in sufficiently moist substrate and stabilization of the tunnels with a lining of mucus were observed by Gelder (1984). Considerable amounts of silica particles in the gut contents of enchytraeids have been reported (e.g., O'Connor, 1967; Babel, 1968; Toutain et al. 1983; Gelder, 1984; Didden, 1990). Together with mineral particles attached to the body surface (Ponge, 1984), enchytraeids transport these particles and may in this way influence soil structure. A field experiment with artificial soils (Didden, 1990) showed a significant effect of *Enchytraeus buchholzi* on air permeability, pore structure, and aggregate stability, even though the estimated amount of mineral soil transported by this species through ingestion was low.

E. Role of Enchytraeids in Phytopathological Interactions

Little or no conclusive evidence exists concerning noxious effects of enchytraeids on plants. Harker (1889) and Stoklasa (1897) reported that potworms damage sugar beet plants, but this has never been reconfirmed. Gordon Hewitt (1908) and Kurir (1964) found that *Fridericia* species were a pest on young conifer plants (*Fridericia bisetosa* on larch and *Fridericia galba* on fir, respectively), from which they consumed the bark just above the roots. Kurir (1964) related this finding to unusually high populations of this species in the compost used in the tree nursery. Conversely, potworms have been found to act antagonistically on pathogenic nematodes on strawberry plants (Jegen, 1920). As long as the plants were not too heavily infected by the nematodes, the presence of enchytraeids worked out favorably.

IV. METHODS TO QUANTIFY ENCHYTRAEIDAE

A. Extraction Techniques

Nielsen (1953) was the first to develop a quantitatively reliable extraction technique for terrestrial enchytraeids. Nowadays the wet funnel extraction method originally proposed by O'Connor (1955, 1962) is the most widely used extraction method for terrestrial Enchytraeidae. Soil samples are placed in a sieve and submerged in a water-filled funnel. By gradually increasing the temperature of the sample to reach a temperature of ca. 40°C after 3 hours, the worms are forced

out of the sample down into the funnel. Variations in duration of the period the sample is left in unheated water, the heating period, and the end temperature are also employed. The efficiency of this technique varies from 95% or more for organic soils (Healy, 1987) to less than 50% (Willard, 1972; Keidel, 1991). The low extraction efficiencies reported by Willard (1972) were found in dry soil, with a low organic matter content. It was assumed that enchytraeids enter an inactive stage under dry conditions and are not able to leave the sample. Low extraction efficiencies were also reported by Healy and Walters (1994) from a North American salt marsh, where large numbers of enchytraeids were found to inhabit leafsheets and stems of *Spartina alterniflora*.

Recently a simpler wet extraction method with an efficiency claimed to be equal to or greater than that of the O'Connor method has been proposed (Graefe, 1973, 1984; Schauermann, 1983). In this modified wet funnel extraction method heating of the sample is omitted, and the extraction time is extended to 48 hours, in some cases up to 2 weeks. This method may yield better results, especially with soil samples from meadows and beech forests, but the prolonged extraction time may be a drawback when large numbers of samples must be processed (Schauermann, 1983; Didden et al., 1995).

B. Identification of Species

Nielsen and Christensen (1959) proposed a set of criteria for description and identification based on internal organizational features, and Dózsa-Farkas (1992) presented a concise list of these parameters and the necessary elements for a species description (Table 4; see also Fig. 1). Keys to the identification of genera were provided by Nielsen and Christensen (1959), O'Connor (1967), and Dash (1983, 1990). Yet, identification to species remains difficult because of the large intraspecific variation, the frequent appearance of new species descriptions, and the requirement that species have to be identified alive and for most species only mature specimens can be identified with certainty. Consequently, relatively few investigators are capable of doing research on the species level. This hampers progress in enchytraeid ecological knowledge. For the description and identification of some species of the genus *Enchytraeus* recent techniques such as ultrastructural and isoenzyme analysis and the study of protein patterns and deoxynucleic acid (DNA) restriction fragment length patterns have been employed (e.g., Brockmeyer, 1991; Schlegel et al., 1991; Westheide et al., 1991). With these techniques new *Enchytraeus* species that could otherwise not be distinguished (Westheide and Graefe, 1992) have been described. Ecological differences between these species are still unclear, however.

Table 4. Parameters for the Identification and Description of Enchytraeidae

Descriptions	Drawings
1. Size (length in mm; alive and preserved)	A. Necessary in all cases
2. Number of segments	1. Setae
3. Color (due to —)	2. Lymphocytes
4. Habitus (e.g., flattened body, slow motions)	3. Nephridia
5. Cutaneous glands (how many per segment, position, clearly visible or only after staining)	4. Sperm funnel
6. Setae or setal follicles (presence, form, length, number per bundle, shape of bundle, setal formula according to Nielsen and Christensen, 1959)	5. Spermatheca
7. Clitellum (on segments—, form, arrangement of the cells)	6. Penial bulb
8. Septal glands (number, primary or secondary, form (lobes?, united?))	
9. Esophageal or gut appendages (size, form, segments—)	B. Necessary in some cases 1. Habitus
10. Chloragogen cells (appearance, size, beginning in segment—)	2. Clitellum
11. Lymphocytes (size, shape, color, granulation, attached to—)	3. Esophageal or gut appendages
12. Brain (form, especially the posterior edge, size)	4. Septal glands
13. Peptonephridia (form, length)	5. Brain
14. Nephridia (form, ratio pre- to postseptale, site of duct origin, number of preclitellar nephridia)	6. Peptonephridia
15. Dorsal vessel (blood color, origin, hearts?)	
16. Penial bulb (presence, size, form, surrounding glands, tuberculae pubertatis?)	For new descriptions also essential
17. Seminal vesicle (presence, located in segments—, size)	1. Methods used in description
18. Spermatheca (presence, size, form, located in segments—, attached or free, number and form of diverticula, ratio of length of duct and ampulla, form and location of glands, presence of spermatozoa)	2. Sampling date and site of holo- and paratypes

Table 4.   (continued)

Descriptions	Drawings
19. Sperm funnel (size, form, length of duct, form of the collar)	3. Collection number and location of holo- and paratypes
20. Egg number	4. Habitat characteristics
21. Additional observations	5. Ecological data (e.g., vertical distribution)
	6. Comparison and valuation with other species in genus

Source: Dózsa-Farkas (1992).

C. Experimental Methods

1. Cultivation of Enchytraeids

The culturing of enchytraeids is problematic, except for species of *Enchytraeus* and *Lumbricillus* and *Cognettia sphagnetorum*. *Enchytraeus albidus* is even being cultured commercially as fish food (Ivleva, 1969). Most species can survive for quite a while under laboratory conditions but fail to reproduce satisfactorily. Improved cultivation methods by offering more natural media, particularly those based on soil composition, have recently produced better results with *Fridericia bulboides*, *Buchholzia appendiculata*, *Henlea perpusilla*, *Henlea ventriculosa*, and *Marionina clavata* (Didden, unpublished).

2. Experimental Designs for Studying Enchytraeid Activity

Methods in ecological research on potworms do not differ fundamentally from those applied to other soil faunal groups (Chapters 4, 6–9). A direct observational method was developed by Christensen (1956), who used small culture chambers consisting of two microscope slides, separated by cardboard or filter paper and filled with culture medium. The small distance between the slides allowed observation of enchytraeid activities such as feeding and cocoon deposition. A way of observing enchytraeids in a more natural habitat was applied by Head (1967), who used time-lapse photography in a large rhizotron. With this technique it was possible to observe the feeding and locomotory activities of potworms in relation to root development. Direct observations on enchytraeids have mostly been done in laboratory studies, using microscopic techniques (for instance, the studies of

feeding and tunneling behavior by Gelder (1984)). Yet, interpretation of such observations requires caution because laboratory conditions may differ greatly from field situations.

An indirect way to study enchytraeid activities is the use of gnotobiotic microcosms or mesocosms in which, for example, respiration, leaching, or change in soil structure with and without potworms may be recorded (among others Wolters, 1988; Abrahamsen, 1990; Setälä et al. 1991). Although gnotobiotic systems are valuable for ecological research and the development of theory, the results require validation in the field. Several agricultural research projects on the biological functioning of the soil system which included enchytraeids have been carried out. Among them are the Polish project "Ecological Effects of Intensive Agriculture" (Ryszkowski, 1974), the Swedish "Arable Land Project" (Andrén, 1988), and the Dutch "Programme on Soil Ecology of Arable Farming Systems" (Brussaard et al., 1988). Generally, such projects are aimed at the development of sustainable agriculture. For this, focus is on the effects of variations in management practices such as soil tillage, fertilization, and pest control on the composition and functioning of the soil community, and on the yield. Activity and functioning of soil fauna in these systems usually are evaluated by field measurements of abundances and biomasses of the various faunal groups in combination with (literature) data on ecological efficiencies, respiratory metabolism, population turnover, and other factors (Golebiowska et al., 1974; Paustian et al., 1990; Didden et al., 1994).

V. AGRICULTURAL MANAGEMENT AND ENCHYTRAEIDAE

A. Soil Cultivation

Physical habitat changes that may influence enchytraeid communities may be specifically demonstrated in arable soils. Important in this respect are effects of changes in soil structure, in the amount of primary production reaching the soil as dead organic material, and in plant species diversity. King and Hutchinson (1976, 1983) and Hutchinson and King (1980) studied the effects of sheep stocking intensity on invertebrate communities in Australian pastures. Enchytraeid numbers, biomass, and activity were inversely related to grazing pressure. The effects could mainly be attributed to soil compaction, resulting in a reduction in habitable pore space, changes in microclimatological regimes, and a reduction in food supply. Brockmann et al. (1980) also reported a significant reduction of enchytraeid densities in a field experiment with soil compaction. Effects of soil tillage are most distinct when the top soil is inverted. Several investigators (Lagerlöf et al., 1989; Nakamura, 1989; Didden, 1991) reported a more even vertical distribution of Enchytraeidae in ploughed plots, where in no-till plots the

enchytraeids mainly occurred in the upper soil layer. Because by ploughing plant residues are transferred to deeper soil layers, there even may occur concentrations of enchytraeids at this depth. Effects of soil tillage on vertical distribution may be persistent and have even been recorded after at least 25 years (Tomlin and Miller, 1987). As opposed to earthworms (Chapter 6), soil tillage seems to have little or no detrimental effect on potworm abundances. There even are indications that soil tillage may positively influence enchytraeid abundances (Fründ et al., 1992; Didden et al., 1994). The smaller size of enchytraeids, their higher population growth rates, and less disturbance of their microhabitats by tillage probably make them less vulnerable than earthworms.

B. Fertilizers

Enchytraeids, like most other soil faunal groups, depend on dead organic matter. Therefore, it is not surprising that generally higher (up to two or three times) abundances of potworms are reported from sites where organic fertilizers, such as crop residues, compost, and manures, are applied (e.g., Alejnikova et al., 1975; Kitazawa and Kitazawa, 1980; Andrén and Lagerlöf, 1983). Springett (1994), on the other hand, found fewer enchytraeids, but a greater species diversity, in organically as compared to conventionally managed sites in New Zealand.

Application of inorganic fertilizers may affect enchytraeid communities. directly through changes in electrical conductivity of the soil solution (Heungens, 1984), and indirectly through the influence on primary production and soil microclimate (see Chapter 2). An initial negative shock effect followed by an increase in enchytraeid numbers has repeatedly been observed (e.g., Huhta et al., 1967; Nakamura, 1988). Marshall (1974) reported significantly lower densities and a more downward distribution of enchytraeids in coniferous forest after a single application of urea. From Polish meadows fertilized yearly with 680 kg ha^{-1} NPK, similar effects were reported, and there were also indications of a changed species composition (Makulec, 1976). These results were mainly attributed to an alteration of the soil moisture regime that occurred in the fertilized meadows. Standen (1984) showed that enchytraeid biomass in fertilized hay meadow plots was negatively correlated with phosphorus fertilization, but did not find a correlation with organic fertilization or nitrate. In an earlier study Standen (1982) found negative correlations between the number of enchytraeid species and the applied amount of nitrate and sodium.

Application of inorganic fertilizers generally results in higher primary production, but apparently enchytraeid populations do not always benefit from their use. There may be various reasons for this: (1) an initial shock effect may occur through direct toxic effects or changes in the soil microclimatological regime, resulting in lower population densities and possibly a changed species

composition; (2) in most cases where fertilizers are applied, the majority of primary production is removed, causing less dead organic material to enter the soil system; (3) fertilizer applications often result in less diverse plant communities and hence less diverse lead organic material, reducing the number of niches for soil organisms. Thus, it may be expected that application of inorganic fertilizers occasionally results in temporarily higher population densities of enchytraeids, but in all cases in a reduced species diversity. Moreover, it has been found repeatedly that after application of inorganic fertilizers enchytraeids show a more downward distribution; nutrients mineralized through their activity may more easily be lost from the system. In other soil faunal groups comparable effects may occur (see Chapter 3–9).

C. Pesticides

The effects of pesticides on enchytraeid communities may be separated into short-term and long-term effects. Short-term effects are direct toxic effects or changes in the physical and chemical properties of the environment and last as long as the pesticide is present. Long-term effects occur through changes in composition of the soil community or the physical environment, or genetic adaptation within populations.

Toxic effects of the herbicide (2,4,5-Trichlorophenoxy) acetic acid (2,4,5-T) on enchytraeid species have been observed in laboratory experiments by Römbke (1988). The effects were species-dependent: *Enchytraeus albidus* was less sensitive than *Cognettia sphagnetorum, Marionina cambrensis,* and *Achaeta* cf. *affinis.* The toxic effect was greater in more acid substrates. In field experiments conducted in a beech forest, treated bimonthly over two years with 2,4,5-T, these results were only partly corroborated (Römbke, 1988): *Cognettia sphagnetorum* apparently was hardly influenced. After 2,4,5-T application had stopped, enchytraeid numbers temporarily increased and they returned to the control level after 2 years. Similar observations, with Paraquat[1] and Simazine[2] in forest sites, and with Atrazine[3] in an orchard, were made by Bäumler et al. (1978) and Chalupsky (1989). Thus, a single application of a herbicide initially may reduce enchytraeid numbers, followed by temporarily increased population densities, presumably due to extra availability of dead plant material. Other soil faunal groups such as nematodes, mites, and collembola may exhibit similar reactions (Bäumler et al., 1978; Andrén and Lagerlöf, 1983) (see also Chapters 3, 4, 6–9). Repeated application of herbicides may lead to a permanent decrease of enchytraeid densities and diversity, as a result of the reduction in weed production and plant species diversity.

Studies addressing the effect of fungicides on potworms are scarce. In a laboratory experiment Benomyl[4] reduced fertility and hatching success with two *Enchytraeus* species (Bethke-Beilfuß and Westheide, 1987). Low dosages of

Benomyl and Pentachlorophenol (PCP) in the laboratory produced considerable mortality with *Enchytraeus albidus*, and *Cognettia sphagnetorum, Marionina cambrensis*, and *Achaeta* cf. *affinis* were even more sensitive to PCP (Römbke, 1988, 1989). However, in field experiments with regular applications of Benomyl even a slight increase in enchytraeid numbers, possibly related to reduced numbers of earthworms, may be observed (Niklas, 1980; Andrén and Lagerlöf, 1983). From the probable food relation between fungi and potworms, negative indirect effects of fungicides would be expected. That such effects were not found in all cases might be explained by little food selectivity in the species concerned, or a shift toward less selective species.

Some insecticides and nematicides, such as Parathion,[5] Carbofuran,[6] and Terbufos,[7] produced short-term toxic effects on potworms in laboratory experiments (Bethke-Beilfuß and Westheide, 1987; Römbke, 1989). Field trials with insecticides, acaricides, and nematicides have shown neutral, positive, as well as negative effects on enchytraeid populations (Didden, 1991). Aldrin,[8] DDT,[9] Aldicarb,[10] and Phenamiphos[11] caused no effects (Edwards et al., 1967; Heungens, 1970; McColl, 1984); Phorate[12] and Lindane[13] were reported to promote enchytraeid populations, possibly because predators or competitors were reduced (Way and Scopes, 1968; Kitazawa and Kitazawa, 1980); and Lindane, Aldicarb, Dazomet,[14] Toxaphene[15] and 1,3-dichlorodipropene (D-D) affected enchytraeids adversely (Huhta et al., 1967; Edwards and Lofty, 1971; Bäumler et al., 1978; Didden, 1991). In general, most insecticides, acaricides, and nematicides probably produce short-term (up to several months) negative effects on enchytraeid densities. In some cases, however, higher potworm densities may eventually result. Since little or no research has been conducted on the species level it remains unclear whether application of pesticides may cause a shift in species composition and/or functioning of the enchytraeid community.

D. Crop Rotations

Investigations on the effects of crop rotations on enchytraeid populations are scarce. Largest populations probably occur in root crops (Ryl, 1977; Kasprzak, 1982; Didden, 1991), and inclusion of leys in a rotation was shown to have a positive effect on population densities (Ryl, 1977; Lagerlöf et al., 1989). The amount and quality of fresh organic material entering the soil presumably determine the size and composition of the enchytraeid community.

VI. POSTSCRIPT

Enchytraeids are an important faunal component in many agricultural systems, and any adverse effect of these worms is unlikely. A significant portion of the

nutrients in the system pass through the enchytraeid populations and are temporarily stored in their tissues. Since their population dynamics may entail a release of these stored nutrients when there is less demand from the crop, more knowledge on soil tillage and the use of catch crops are needed to prevent a possible loss of nutrients. Potworms significantly contribute to a stable soil structure and a favorable pore size distribution, although on a smaller scale than earthworms. The lack of methods to manipulate enchytraeid populations hampers successful use of potworms in sustainable agricultural production. A general rule of thumb may be that an agricultural system with shallow or no tillage and a large pool of organically bound nutrients favors enchytraeids most, and puts them to use for crop production. Table 5 lists possible effects of reduced agricultural inputs on enchytraeid populations. Enchytraeids could also profitably be used as indicator organisms because of clear interspecific differences in responses to environmental conditions and the usually short generation time. Prerequisites

Table 5. Possible Effects of Reduced Agricultural Inputs

Diminishing Intensity of	Leads to
Tillage	Increase of earthworm abundance → decrease of enchytraeid abundance by competition (?)
Shallower	Differentiation of soil profile → (relative) increase of enchytraeid abundance in upper layer
Less often	Development of litter layer → appearance of additional litter-dwelling species
Fertilizer application	
General reduction	Decrease of plant biomass → decrease of enchytraeid abundance
Relatively more organic fertilizer	Development of humus → increase, particularly of eutraphent species
Crop spacing	
In space	Microclimatic mosaic → higher species diversity (?)
In time (more fallow periods)	Successional dynamics → appearance of specific species (?)
Pest control	
Less, more specific pesticides; accepting higher yield losses	Higher trophic complexity, lower toxic load → higher stability and vitality of populations?

Source: Fründ and Graefe (1992).

to use of potworms in sustainable agriculture and as indicator organisms are better development of enchytraeid taxonomy and increased number of trained researchers able to identify potworms to species.

Notes

1. Paraquat: 1,1'-Dimethyl-4,4'-bipyridinium
2. Simazine: 6-Chloro-*N,N*'-diethyl-1,3,5-triazine-2,4-diamine
3. Atrazine: 6-Chloro-*N*-ethyl-*N*'-(1-methylethyl)-1,3,5-triazine-2,4-diamine
4. Benomyl: methyl-*N*-benzimidazol-2-yl-*N*-(butylcarbomoyl)carbamate
5. Parathion: *O,O*-diethyl *O*-p-nitrophenyl phosphorothioate
6. Carbofuan: 2,3-dihydro-2,2-dimethyl-7-benzofuranyl methyl carbamate
7. Terbufos: *s-tert*-butylthiomethyl *O,O*-diethyl phosphorodithioate
8. Aldrin: 1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-endo-1,4-exo-5,8-dimethanonaphtalene
9. DDT: 1,1,1-trichloro-2,2-bis(p-chlorophenyl)-ethane
10. Aldicarb: 2-methyl-2(methylthio)propionaldehyde *O*-(methylcarbamoyl) oxime
11. Phenamiphos: ethyl-4(methylthio)-*m*-tolylisopropyl-phosphoro-amidate
12. Phorate: diethyl S-(ethylthiomethyl) phosphorothiolothioate
13. Lindane: gamma isomer of 1,2,3,4,5,6-hexachlorocyclohexane
14. Dazomet: tetrahydro-3,5-dimethyl-2H-1,3,5-thiadiazine-2-thione
15. Toxaphene: octachlorocamphene

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