

Changes in the Assemblage of Necrophilous Invertebrates under the Effect of Pollution with Emissions from the Middle Ural Copper Smelter

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Abstract—Changes in the abundance and taxonomic and trophic structure of necrophilous invertebrates inhabiting mixed forests have been studied in the area polluted with the emissions from the Middle Ural Copper Smelter. It has been shown that the abundance of most taxa decreases by factors of 2 to 80 along the pollution gradient, but the trophic structure and composition of major groups vary insignificantly. Changes in the necrophilous assemblage can be caused by either direct (toxic) action of industrial pollutants or their indirect effect exerted through modification of habitats.

Keywords: necrophilous invertebrates, population structure, industrial pollution, heavy metals, copper smelter, the Middle Urals, forest ecosystems

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Decaying animal remains attract numerous invertebrates, which are referred to as the cadaveric fauna, or necrophilous complex (Fuller, 1934; Putman, 1978). Initial interest in these invertebrates and subsequent history of studies on them were based on their practical significance for forensic assessment. Over more than a century, forensic entomology has developed into an independent scientific discipline that is still progressing (Méglin, 1894; Current Concepts..., 2010). Most studies in this field are based on the experimental approach where observations are performed on dead bodies exposed to necrophages, usually those of large animals (e.g., pigs or dogs) intended to simulate a human corpse. Less developed are field studies on the communities of necrophilous invertebrates (Fuller, 1934; Lyabzina, 2003), which have shown that the complex of organisms utilizing organic matter from corpse tissues is an integral part of the majority of natural terrestrial and aquatic ecosystems.

The improvement and interpenetration of the two approaches have given rise to studies on the composition and biological characteristics of major necrophilous groups, detailed analysis of microsuccessional changes in the composition of invertebrates during utilization of cadaveric organic matter (Nabağlo, 1973; Putman, 1978; Braack, 1987; Kočárek, 2003), and development of an ecological classification of the cadaveric fauna. It has been shown that typical necrophages that utilize cadaveric organic matter and thereby facilitate the return of biogenes into the bio-

logical cycle are not the only members of the necrophilous complex. This complex also includes a significant proportion of predatory and parasitic species feeding on other invertebrates and, in addition, of species consuming mold fungi (Marchenko, 1980; Braack, 1987; Kozminykh and Eshunin, 1994). These groups are of significance as entomophages controlling the larval abundance of dipterans, which are vectors of many infectious diseases, but they themselves can play the role of such vectors.

In a number of studies published in the recent decades, necrophilous invertebrates have been used to evaluate anthropogenic impact on the biota. The range of anthropogenic factors they address includes recreational activities and urbanization (Wolf and Gibbs, 2004; Ereemeev and Psarev, 2010), as well as emissions from motor transport (Butovskii, 1990) and various industries (Freitag and Hastings, 1973; Zvereva, 1993; Sigida and Pushkin, 2002; Kozlov et al., 2005; Prisnyi, 2009). In the majority of cases, these studies concern only one particular taxonomic group and are often limited to comparisons between the faunistic lists for disturbed and background areas, but some of them provide data on the accumulation of toxic agents (Butovskii, 1990; Nuorteva and Nuorteva, 1982) or morphological and physiological abnormalities in the bodies of invertebrates (Sigida and Pushkin, 2002; Prisnyi, 2009). There are only sporadic publications dealing with the effect of anthropogenic pollution on the abundance of particular groups of necrophilous

invertebrates (Freitag and Hastings, 1973; Zvereva, 1993; Kozlov et al., 2005), whereas its effect on their complex as a whole has been not studied at all.

MATERIAL AND METHODS

Studies were performed in the area exposed to emissions of airborne pollutants (mainly polymetallic dust and sulfur dioxide) from the Middle Ural Copper Smelter (MUCS) located in the vicinity of Revda, Sverdlovsk oblast. The study area is described in detail in previous publications (Vorobeichik et al., 1994; *Ekologicheskaya toksikologiya...*, 2001; Zolotarev and Bel'skaya, 2012). Technogenic degradation of forest ecosystems under the impact of these emissions is accompanied by an increase in toxicity of the litter (compared to the background values, the concentrations of mobile forms of Cu, Pb, Cd, and Zn are higher by factors of 200, 45, 15, and 6, respectively), its acidity (pH drops from 6.1 to 5.5), and depths (by a factor of 2–3), as well as by reduction in the coverage of the herb–dwarf shrub layer (from 80 to 15%), with consequent changes in microclimate (higher insolation and disturbances in the thermal and moisture regimes). Ecotoxicological investigations of invertebrate communities in this area have been performed for more than 20 years. During this period, the quantitative data on possible responses to pollution have been obtained for the groups of soil macrofauna (Vorobeichik, 1995; Vorobeichik et al., 2012), herpetobions (Ermakov, 2004; Zolotarev and Bel'skaya, 2012), and chortobions (Vorobeichik et al., 1994; Nesterkov and Vorobeichik, 2009).

Trapping censuses were taken during the summer months of 2003 (July 20–August 8), 2004 (July 16–August 18), and 2005 (May 18–June 16) in secondary mixed forests with dominance of birch in three zones located west from the MUCS (opposite to the prevailing wind direction) at different distances: 1 km (the impact zone), 6 km (the buffer zone), and 16 km (the background zone). Three test plots (in 2003, one plot) were laid in each zone to set traps for invertebrates. The trap of original design (Ermakov, 2013) consisted of a transparent plastic bottle with openings in its side walls, bait suspended inside, and a removable sample container with fixative (1% formaldehyde solution) attached to the bottle neck from below. Invertebrates attracted by the bait enter the trap through the openings and, trying to get out, fall down into the sample container. In each plot, 5–8 traps were hung in line 1.5 m above the ground at 30-m intervals. Dead vivarium house mice weighing 20–30 g were used as bait. Two traps were left unbaited in order to use these samples as reference for determining whether the collected invertebrates belonged to the necrophilous complex or were trapped accidentally. The traps were examined to collect the catch every 7–8 days, the total exposure period was 29–33 days. During this period, the bait passed all major stages of postmortem micro-

succession: from colonization by necrobionts and active decomposition to early stages of mummification and loss of attractiveness to invertebrates.

The work performed over three seasons amounted to 3352 trap–days, and about 50000 invertebrates of different species were collected. The samples were sorted out in the laboratory. All invertebrates were counted visually, except for small forms with a body length of less than 2 mm, such as phoretic acariform mites, feather-winged beetles, dipteran eggs and first instar larvae. The abundance was expressed as the number of specimens per trap over the entire exposure period. Data from broken or damaged traps were excluded from analysis.

RESULTS

The complex of necrophilous invertebrates inhabiting the study area consisted of insects and arachnids, but the abundance and diversity of the former were significantly higher. Insects attracted by bait belonged to ten orders, with the core of the complex being formed by the Diptera and Coleoptera (Table 1).

Dipterans were mainly of the suborder Brachycera Cyclorrhapha (fam. Calliphoridae, Sarcophagidae, Piophilidae, Muscidae, Fanniidae, Phoridae, Anthomyiidae, Sepsidae, Heleomyzidae): their proportion in the necrophilous complex reached 30–60% or, considering larval stages, even 60–85%. Other Brachycera (fam. Mycetophilidae, Sciaridae, and some others) were not numerous in our samples.

Necrophilous coleopterans (studied in more detail) were represented by 13 families, with representatives of the superfamily Staphylinoidea (Silphidae, Staphylinidae, and Cholevidae) accounting for more than 70% of the total abundance of these insects. Other coleopteran families, with rare exceptions (fam. Nitidulidae) were represented by single specimens. The remaining orders (Hymenoptera, Heteroptera, Mecoptera, Psocoptera, Lepidoptera, Orthoptera, Neuroptera, Dictyoptera) comprised less than 10% of the total abundance of invertebrates. Arachnids found on bait were individual harvestmen (fam. Phalangidae) and more numerous spiders (fam. Philodromidae and Salticidae), which moved to the traps out of tree crowns and preyed on insects (mainly adult small dipterans) landing on bait.

The range of trophic groups of necrophilous invertebrates, which is presented in a simplified variant, includes not only various forms specialized in feeding on carrion at different stages of decay (schizophages consume fluids and liquefied necrotic tissues; sarconecrophages, soft tissues; keratophages, keratinized and dry remains) but also predators and mycetophages (Table 1). Species with a mixed type of feeding, such as zoonecrophages, were included in different groups depending on their preferred food object. Parasitic species were attributed to zoophages, and species with still other trophic specialization were placed in the

Table 1. Taxonomic and trophic structure of necrophilous invertebrates along the pollution gradient

Groups of invertebrates	2003			2004			2005		
	Background (n = 5)	Buffer (n = 5)	Impact (n = 5)	Background (n = 15)	Buffer (n = 14)	Impact (n = 15)	Background (n = 15)	Buffer; (n = 18)	Impact (n = 18)
Taxonomic groups, number of specimens over the exposure period (<i>m</i> ± <i>SE</i>)									
Diptera, imago	132.8 ± 11.2	87.3 ± 22.1	70.4 ± 15.1	128.6 ± 16.6	95.2 ± 13.8	60.6 ± 8.1	345.8 ± 36.3	467.3 ± 51.1	298.9 ± 51.5
Diptera, larvae & pupa	29.0 ± 7.3	142.3 ± 23.8	164.4 ± 10.9	108.8 ± 18.1	176.3 ± 29.0	47.7 ± 8.5	78.5 ± 14.1	134.0 ± 21.4	112.7 ± 15.4
Coleoptera	100.6 ± 22.1	30.75 ± 5.3	14.2 ± 1.9	88.9 ± 14.0	73.0 ± 12.0	36.4 ± 6.2	261.0 ± 28.2	115.2 ± 9.1	57.2 ± 7.4
Including:									
Silphidae	71.0 ± 14.5	16.6 ± 4.7	1.8 ± 1.3	57.7 ± 10.1	21.8 ± 4.9	5.5 ± 1.5	153.6 ± 19.6	61.1 ± 5.1	22.9 ± 4.1
Staphylinidae	19.0 ± 5.8	8.7 ± 1.7	7.6 ± 2.3	13.4 ± 2.2	40.2 ± 7.2	24.5 ± 5.5	32.9 ± 3.7	13.7 ± 1.7	15.8 ± 2.5
Cholevidae	5.0 ± 2.6	1.5 ± 1.024	—	9.6 ± 2.4	3.7 ± 0.9	0.3 ± 0.1	47.1 ± 10.0	33.8 ± 5.6	4.5 ± 2.0
Histeridae	—	—	—	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	2.9 ± 0.8	1.4 ± 0.4	1.6 ± 0.3
Nitidulidae	1.4 ± 0.7	0.9 ± 0.4	1.4 ± 1.4	2.5 ± 0.7	2.1 ± 0.4	1.1 ± 0.4	16.0 ± 2.5	0.9 ± 0.3	0.2 ± 0.1
Dermeestidae	1.0 ± 0.4	0.2 ± 0.2	0.2 ± 0.2	—	1.2 ± 0.7	0.3 ± 0.2	1.1 ± 0.4	1.0 ± 0.3	5.7 ± 1.6
Latridiidae	2.2 ± 1.0	1.7 ± 0.5	1.8 ± 1.3	2.4 ± 0.5	1.9 ± 0.3	4.0 ± 1.0	4.7 ± 0.9	1.8 ± 0.5	4.4 ± 0.9
other families	1.0 ± 0	1.3 ± 0.2	1.4 ± 0.5	3.3 ± 0.6	2.1 ± 0.5	0.7 ± 0.3	2.6 ± 0.6	1.5 ± 0.3	2.1 ± 0.4
Heteroptera	2.0 ± 0.3	1.0 ± 0.4	2.2 ± 1.1	10.0 ± 2.4	5.0 ± 0.7	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Psocoptera	1.6 ± 0.6	1.0 ± 0.5	0.2 ± 0.2	1.7 ± 0.4	0.8 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.2
Mecoptera	1.4 ± 1.2	1.4 ± 0.6	1.4 ± 1.0	2.3 ± 0.4	5.4 ± 1.3	2.9 ± 0.9	0.3 ± 0.1	0.3 ± 0.1	0.6 ± 0.3
Lepidoptera	3.0 ± 0.5	0.5 ± 0.2	1.6 ± 0.9	0.5 ± 0.2	0.9 ± 0.2	0.7 ± 0.4	2.1 ± 0.5	0.3 ± 0.2	0.4 ± 0.2
Hymenoptera	1.2 ± 0.5	6.9 ± 1.8	1.2 ± 0.6	1.3 ± 0.3	8.9 ± 3.0	6.8 ± 2.4	1.4 ± 0.5	28.8 ± 16.5	52.9 ± 30.0
others Insecta	0.4 ± 0.2	—	1.0 ± 0.3	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	—	0.3 ± 0.1
Arachnida	1.8 ± 1.0	0.4 ± 0.4	0.4 ± 0.2	1.4 ± 0.3	1.2 ± 0.3	2.9 ± 0.6	0.4 ± 0.2	0.3 ± 0.1	1.1 ± 0.2
All groups	273.8 ± 35.3	271.4 ± 31.0	257.0 ± 22.6	343.6 ± 24.7	367.0 ± 36.0	158.2 ± 16.5	689.9 ± 48.4	746.7 ± 60.3	524.6 ± 58.1
without preimaginal Diptera	244.8 ± 32.9	129.1 ± 28.6	92.6 ± 18.0	234.8 ± 26.6	190.6 ± 22.4	110.5 ± 12.4	611.4 ± 52.9	612.7 ± 59.9	411.9 ± 51.4
Trophic groups, %									
Necrophages	89.3	92.0	93.5	89.4	82.3	75.4	90.8	93.6	82.7
Including:									
schizophages	62.3	85.7	92.6	71.2	74.5	71.1	62.4	80.5	76.3
sarconecrophages	26.7	6.3	0.8	18.2	7.4	4.1	28.3	13.0	5.0
keratophages	0.3	0.1	0.1	0.0	0.4	0.1	0.1	0.1	1.4
Zoophages	8.2	6.2	4.3	7.6	15.6	20.3	5.7	5.8	15.6
Mycetophages	2.0	1.3	1.1	2.0	1.4	3.8	3.1	0.4	1.1
others	0.6	0.5	1.0	1.0	0.7	0.5	0.5	0.2	0.6

Figures in parentheses show sample size (a trap is an accounting unit). Dash indicates the absence of a group.

Table 2. Results of two-way ANOVA for differences in the abundance and proportions of trophic groups of necrophilous invertebrates in test plots

Group	Source of variation					
	Pollution zone ($df = 2, df_{Error} = 107$)		Year of sampling ($df = 2, df_{Error} = 107$)		Zone \times year ($df = 4, df_{Error} = 101$)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Taxonomic groups (based on abundance)						
Diptera, imago	8.09	0.001	80.88	<0.001	1.78	0.138
Diptera, larvae & pupa	7.40	0.001	0.02	0.985	5.85	<0.001
Coleoptera	39.88	<0.001	28.82	<0.001	2.21	0.073
Including:						
Silphidae	68.10	<0.001	30.67	<0.001	1.34	0.259
Staphylinidae	2.46	0.091	4.52	0.013	6.89	<0.001
Cholevidae	39.68	<0.001	49.56	<0.001	3.32	0.013
Histeridae	0.54	0.586	48.82	<0.001	1.11	0.355
Nitidulidae	26.11	<0.001	4.99	0.009	19.53	<0.001
Dermestidae	1.15	0.322	12.49	<0.001	4.54	0.002
Latridiidae	1.69	0.190	2.09	0.129	1.70	0.155
other families	1.81	0.169	0.57	0.568	3.40	0.012
Heteroptera	12.48	<0.001	53.78	<0.001	16.45	<0.001
Psocoptera	9.12	<0.001	8.74	<0.001	5.81	<0.001
Mecoptera	1.28	0.284	32.78	<0.001	1.31	0.273
Lepidoptera	9.59	<0.001	4.38	0.015	6.50	<0.001
Hymenoptera	8.67	<0.001	2.01	0.139	2.20	0.074
others Insecta	6.99	0.001	4.40	0.015	3.19	0.016
Arachnida	3.15	0.047	12.10	<0.001	1.70	0.156
All groups	12.60	<0.001	80.35	<0.001	4.06	0.004
Without preimaginal Diptera	18.15	<0.001	95.36	<0.001	1.46	0.221
Trophic groups (based on proportion in the complex)						
Necrophages	2.13	0.125	10.90	<0.001	2.96	0.023
Including:						
schizophages	16.07	<0.001	3.71	0.028	4.67	0.002
sarconecrophages	76.29	<0.001	8.86	<0.001	2.86	0.027
keratophages	1.73	0.182	2.96	0.056	4.12	0.004
Zoophages	2.03	0.136	3.18	0.046	1.28	0.282
Mycetophages	6.73	0.002	5.19	0.007	7.64	<0.001
Others	1.33	0.269	3.62	0.030	1.83	0.130

F, Fisher's test; *p*, significance level; a trap is an accounting unit. Transformation of variables: for abundance, $y = \ln(x + 1)$; for proportions, arcsine transformation. Significant differences ($p < 0.05$) are in boldface.

group designated "others." The proportion of necrophages in the complex exceeded 75%, which was due mainly to the high abundance of schizophages (Diptera); the proportions of sarconecrophages (numerous Silphidae, Cholevidae) and predators (Staphylinidae, Hymenoptera) were considerably lower.

The abundance of major insect groups, adult Diptera and Coleoptera, decreased along the gradient of toxic load by factors of 1.1–2.0 and 2.5–7.0, respectively (Tables 1, 2). The most significant decrease was recorded in burying beetles (by a factor of 7–40), cholevid beetles (by a factor of 10–30), and sap beetles

(by a factor of 80). Predatory coleopterans of the families Staphylinidae and Histeridae showed a higher level of pollution tolerance. Their abundance either remained almost unchanged along the pollution gradient or varied in different directions from year to year. The high abundance of dipteran larvae in samples from polluted plots was apparently explained by alleviation of competition for food with necrophagous beetles and, in turn, provided for a 5- to 40-fold increase in the abundance parasitic and predatory hymenopterans (Braconidae, Pteromalidae, Vespidae, Formicidae) within the impact zone.

Under conditions of pollution, the trophic structure of the necrophilous complex proved to be more conservative than its taxonomic structure. Among all trophic groups, changes were observed mainly in the proportion of sarconecrophages which decreased 4- to 30-fold along the pollution gradient. The proportion of mycetophages also decreased, but less strongly (by a factor of 2–3), while that of schizophages proved to increase in polluted plots. No significant changes in abundance along the pollution gradient were revealed in zoophages, keratophages, and species designated “others” (Table 2).

It should be emphasize that the data obtained in different years diverge from each other. In particular, the abundance of necrophilous invertebrates recorded in 2005 is 3–4 times higher than that in 2003 and 2004. The effect of the factor “year of sampling” was significant in the majority of groups, except for dipterans, hymenopterans, and some small populations of coleopterans (Table 2).

DISCUSSION

The composition and abundance of the necrophilous complex depend on many factors: geographic location of the study area, specific characteristics of the biocenosis, weather conditions, phenological dates, the type and size of bait, the rate of its colonization by invertebrates, etc. (Marchenko, 1992; Kuusela and Hanski, 1982; Holloway and Schnell, 1997; Kočárek, 2003; Anderson, 2010). For this reason, it is difficult to objectively compare the results of the study with published data. However, such a comparison is possible using publications on experiments performed under similar conditions, including geographic location and biocenotic characteristics of the study area, period of trapping, and bodies of small mammals used as bait (Nabaĝlo, 1973; Putman, 1978; Blackith and Blackith, 1990; Isiche et al., 1992; Kočárek, 2003; Lyabzina, 2011).

According to these authors, the core of the necrophilous complex consists of dipterans and coleopterans, as in our case. The former dominate at the initial stages of postmortem microsuccession; the latter, at its final stages. Data on the taxonomic composition of these groups widely vary between publications. For example, the number of Coleoptera species recorded

on small-sized carrion bait varies from several tens of species from the families Silphidae, Staphylinidae and Histeridae (Putman, 1978) to 145 species from 22 families (Kočárek, 2003). Hymenopterans and arachnids, especially mites, are almost always listed as integral components of the necrophilous complex in terrestrial ecosystems. Thus, ants (Formicidae) dominate over dipterans and necrophagous beetles or even totally replace them, both numerically and functionally (Lyabzina, 2011).

The composition of necrophilous complex, as well as development and rate of corpse destruction largely depend on the initial stages of colonization (Putman, 1978; Isiche et al., 1992). It has been noted that this process is largely a matter of chance: different species may succeed in being the first to gain such a rich source of food, and corpses may therefore be colonized by different species complexes (Begon et al., 1989).

It should be taken into consideration that the groups of necrophilous invertebrates and their ratio were determined in our study by using hanging traps, which are inaccessible for nonflying species and restrict access to bait for some other groups. It is known that there are differences in composition between the faunas of suspended corpses and those lying on the surface or buried in the soil (Nabaĝlo, 1973; Marchenko, 1992). The rates of corpse destruction also differ significantly: suspended corpses of large animals are utilized by insects at a lower rate than those lying on the surface and may be preserved over several years (Marchenko, 1992). However, hanging bait does not guarantee that there will be no nonflying invertebrate, especially if they are active “tree climbers” such as ants and spiders.

Almost all relevant publications provide evidence that the abundance of necrophilous invertebrates decreases in polluted or disturbed areas. The only exception concerns the reported increase in the abundance of some saprophilous and necrophilous families of brachycerous dipterans in the area affected by emissions from the Severonikel plant (Zvereva, 1993).

The direct toxic action of pollutants (Nuorteva and Nuorteva, 1982; Butovskii, 1990) and consequent anomalies, reduced viability and fecundity are often regarded the most probable factors responsible for decrease in the abundance of different invertebrate groups (Sigida and Pushkin, 2002; Prisnyi, 2009). However, the increasing number of facts indicate that indirect influences on the invertebrate complexes of impact areas play a more important role (Nesterkov and Vorobeichik, 2009; Zolotarev and Bel'skaya, 2012). Special experiments are needed to resolve this issue.

The observed trend toward a decrease in the abundance of sarconecrophages generally agrees with the pattern of changes described in the trophic structure of soil macrofauna (Vorobeichik, 1995; Vorobeichik

et al., 2012): the proportion of saprophages is reduced as the level of pollution increases, with that of zoophages remaining unchanged or slightly decreasing. Among herpetobiont arachnoids, a decrease in abundance (down to extinction) along the pollution gradient is primarily observed in harvestmen, which are characterized by a mixed type of feeding (zoophagy with some elements of necro- and saprophagy). Spiders (obligate predators) are more tolerant to pollution, and the families Lycosidae and Gnaphosidae even become more abundant as its level increases (Zolotarev and Bel'skaya, 2012). The same situation with harvestmen has been recorded during censuses of invertebrates in the herbaceous layer (Nesterkov and Vorobeichik, 2009). A more intense reaction to chemical pollution is generally typical for saprotrophic invertebrates, either obligate or facultative (Van Straalen and Van Wensem, 1986; Laskowski and Maryński, 1993; Pokarzhevskii et al., 2000).

One of important factors determining the abundance of necrophilous invertebrates is the amount of available food resources (Holloway and Schnell, 1997; Smith and Merrick, 2001; Kozlov et al., 2005). Zvereva (1993) explained high abundance of saprotrophic flies near the Severonikel plant by its proximity to populated areas with household waste dumps, which provide rich food supply to these insects.

The total abundance of small mammals and birds is reduced in technogenically transformed areas near the MUCS. The number of small mammals decreases by half along the pollution gradient: in murine rodents, from 8.6 (background plots) to 4.4 ind./100 trap-days (impact plots) (Mukhacheva, 1996); in shrews, from 1.2 to 1.5 ind./100 trap-days (Mukhacheva, 2007). The total population density and biomass of birds change in a similar way, decreasing from 953 ind./km² (23.5 kg/m²) in the background zone to 510 ind./km² (13.5 kg/m²) in the impact zone (Bel'skii and Lyakhov, 2003). This decline in food resources does not result in the disappearance of the whole complex of degraders but affects mainly its less mobile component, i.e., coleopterans. On the other hand, some authors consider that severe technogenic impact, resulting in increased mortality among vertebrates, thereby improves food supply to necrophages (Kozlov et al., 2005).

Insufficiency of food supply appears to be responsible for the fact that samples collected in the early summer of 2005 contained increased numbers proportion of sap beetles, mainly species feeding on decaying fungi (*Cychramus luteus* F.). The deficit of fungi in forest ecosystems during this period probably makes mycetophages switch to supplementary food resources, including mold on corpses used as bait.

It is impossible to unequivocally explain interannual fluctuations in the abundance of necrophilous invertebrates by the effect of differences in climatic characteristics of the year, calendar and phenological dates of censuses, or other factors. It should be noted,

however, that the data from the nearest meteorological stations (Revda) characterize climatic conditions in 2003 as extremely hot and dry (the daily average temperature over the trapping period 19.2°C, precipitation 33.5 mm) and those in 2005 as cold and moist (15.5°C; 126.8 mm). Moreover, according to the results of theriological studies in the same region (Mukhacheva and Kshnyasev, 2008), the years 2002 and 2005 were attributed to the depression phase (low abundance) in the three-year population cycles of murine rodents; the year 2003, to the growth phase; and the year 2004, to the peak phase. This could have an effect on the total abundance of necrophilous invertebrates recorded in the next year.

The interaction of factors *pollution zone* × *year of sampling* is statistically significant for half of the taxa studied; i.e., their response to pollution differs between years. A possible explanation is that the impact of industrial pollution is partly neutralized by climatic factors. For example, low temperatures and high air humidity retard mummification of bait and allow it to remain attractive to necrophilous invertebrates for a long time, even under "arid conditions" (Nesterkov and Vorobeichik, 2009) of the impact zone. On the other hand, the interaction of these factors is not significant for brachyceran flies and burying beetles, the most abundant and active degraders of corpse organic matter. This is evidence that the response of these groups to pollution is unidirectional, despite climatic differences between years.

Thus, the total abundance of the necrophilous complex in the impact areas decreases by a factor of 2.5–4.0. The decrease in abundance along the pollution gradient is especially strong (30- to 40-fold) among obligate necrophagous coleopterans (burying and cholevid beetles). In contrast, the trophic structure of the complex does not change significantly under the impact of industrial pollution. This is due both to complicated taxonomic structure of the necrophilous complex, with different taxa being characterized by similar trophic preferences, and to the presence of many facultative species that feed on different (supplementary) food resources.

Nevertheless, further strengthening of technogenic impact can minimize or even reduce to zero the role of necrophilous invertebrates in natural communities. If so, the vacant biocoenotic space will be divided between vertebrate scavengers (canids, rats, and crows), which are numerous in the impact areas according to our observations, and unexpended organic necromass apparently will not be accumulated in the litter of impact areas, unlike in the case with leaf debris (Vorobeichik, 1995).

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