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Fauna of ciliates (Alveolata, Ciliophora) of the southern part of the Russian Far East

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Summary

This paper presents information on the distribution of ciliates in freshwater bodies and soils of the southern part of the Russian Far East. During the study, 307 species of ciliated protozoa were registered, 59 of which were identified only to the genus level. The greatest species richness was observed in biotopes of the southern part of Sakhalin Island, watercourses of Primorye, and soils of Middle Priamurye. The core of the ciliate communities (65%) belonged to the classes Oligohymenophorea (86 species), Spirotrichea (69), and Litostomatea (44). In general, faunal diversity of ciliates in natural water bodies was richer than that in anthropogenically transformed water basins. The habitat conditions of ciliates in wastewater treatment plants were not very diverse since some ecological factors therein were artificially controlled by humans. The coefficient of faunistic similarity of ciliates between the surveyed biotopes varied in a wide range (11.7–68.3%). We infer that this fact is caused by the following factors: significant distance between water bodies; similar origin (natural or anthropogenic) and/or belonging to the same river system; influence of some specific environmental factors. However, the zoogeographic analysis of the species community of ciliates from different regions of Russia and beyond did not confirm this hypothesis. During the study, several faunistic complexes of ciliated protozoa were determined in the studied region: eurytopic, including 11 species (*Vorticella convallaria* complex, *V. microstoma* complex, *V. campanula*, *Tachysoma pellionellum*, *Aspidisca cicada*, *Trithigmostoma cucullus*, *Uronema marinum*, *Paramecium aurelia* complex, *Coleps hirtus*, *Chilodonella uncinatus*, and *Spirostomum teres*), and four complexes with species confined to biotopes of just one geographic region.

Key words: ciliates, faunal diversity, freshwater objects, soils, Russian Far East, treatment facilities

Introduction

Free-living ciliates (Ciliophora) is one of the largest groups of unicellular eukaryotes widely distributed in soils, marine and freshwater habitats. Global estimates of the species richness of ciliates are extremely inconsistent and vary from 3 to 40 thousand species, but usually accepted to be 8–9 thousand (Corliss, 2000; Jankowski, 2007). Such a pronounced variation range is due to a variety of methods of collecting and processing of hydrobiological material, short duration of studies, and relatively small amount of molecular data on ciliates (Finlay et al., 1996; Foissner et al., 2003; Foissner et al., 2008; Lynn, 2008).

Up to now, information on the faunistic diversity of ciliates in the Russian Far East has been rather scattered (Nikitina, 1997; Prikhodko, 2009; Tribun, 2012; Zhukov, 2012; Panov, 2015). The aim of this research was to systematize the available data on the biodiversity of soil and freshwater ciliated protozoa in biocenoses of the southern part of the Russian Far East, and to carry out a comparative zoogeographic analysis of the studied ciliate communities with those in different other regions of Russia and beyond.

Material and methods

The samples for studying ciliates were collected by the authors from the following habitats:

- the Amur River (near Khabarovsk) and its small tributaries: the Krasnaya, Chernaya, and Berezovaya Rivers (Tribun, 2021);
- small rivers of the southern part of Sakhalin Island: the Lyutoga, Komissarovka, and Tomarinka Rivers, Bolshoy Takoy (a tributary of the Naiba River); the Krasnosel'skaya, Rogatka Rivers and Prigorodny brook (a tributary of the Sysyja River), and also small lakes in the lower reaches of the Taranai River (Panov, 2015; Panov et al., 2021);
- the soils of the Middle Priamurye: brown taiga illuvial-humus, brown mountain-forest, brown forest, meadow-soddy, and meadow-gleyey (near Khabarovsk, Komsomolsk-na-Amure, and Troitskoye settlement) (Nikitina, 1997);
- aeration tanks of Khabarovsk wastewater treatment facilities (Tribun, 2021); Central City Pond (Khabarovsk) (Tribun et al., 2021).

Besides, we reviewed the data published by the following authors: A.V. Prikhodko (2009) – water treatment facilities of the city Svobodny and the Magdagachi settlement after primary sedimentation,



Fig. 1. Schematic map of the study area

Belogorsk storage pond, brown forest soils of Svobodny, and Gashchenka Lake (Amur region); A.V. Zhukov (2012) – Khabarovsk wastewater treatment facilities at the stage of primary and secondary settling tanks; L.I. Nikitina and Saigina O.N. (2010), O.N. Saigina (2014) – Komarovka River (a tributary of the Razdolnaya River; the region of the villages Kaimanovka and Dubovy Klyuch) and aeration tanks of the Ussuriysk wastewater treatment facilities (Primorsky Krai) (Fig. 1). In total, the area of about 900,000 km² was surveyed: the northernmost (and westernmost) site is the settlement of Magdagachi (53°27' N, 125°48' E); the southernmost is Ussuriysk (43°48' N, 131°57' E); the easternmost is Yuzhno-Sakhalinsk (46°57' N, 142°44' E).

Hydrobiological sampling was performed using samplers (plastic or glass bottles not exceeding the volume of 500 ml), a modified “fouling glass” method (Tribun, 2010), and by scraping periphyton with a soft brush from natural (stones, plant parts) and artificial (submerged objects of anthropogenic origin) surfaces.

For soil samples, we applied the “trap-capsule” technique (Foissner, 1987). During the periods of low ciliate numbers and species diversity, samples were centrifuged (1500 rpm for 30 s). To increase the population of ciliates prior to investigation, the samples were enriched with nutrient substrates: dried banana peels, rice grains, hay broth, etc.

Ciliates were studied *in vivo* and *in vitro* using Leica, Motic, Levenhuk, and Lomo microscopes.

Table 1. Taxonomic structure of ciliate communities of aquatic and soil biotopes of the southern Russian Far East.

Taxon	Sakhalin Island		Primorsky Krai		Amur Region			Khabarovsk Krai			
	Watercourses	Water bodies	Watercourse	Treatment facilities	Water body	Treatment facilities	Soils	Watercourses	Water body	Treatment facilities	Soils
class	11	11	10	7	8	7	6	10	11	8	9
order	24	23	25	15	17	13	10	20	18	16	22
family	50	43	47	22	19	18	14	34	33	31	36
genus	75	61	58	22	25	21	18	44	35	36	53
species	137	106	80	48	39	40	25	64	43	61	91

The cells were observed using the “microaquarium” technique (Dragesco and Dragesco-Kerneis, 1986). For long-term studies (over 20 min), the micro-aquarium was placed in a moist chamber. When working with samples from aeration tanks, we used the “glass by glass” method (Kreutz and Foissner, 2006). Immobilizing solutions of Da-Fano, Carnois, and calcium-formol (according to Baker) were used to decrease the locomotive activity of ciliates. Detection of infraciliature was performed with protargol, general morphology – with 0.1% methylene blue solution, 0.2% eosin solution, and 0.3% iodine solution (Alekperov, 2012; Foissner, 2014).

Species identification of ciliates was performed using identification keys as well as descriptions outlined in monographs and articles: Curds (1975, 1982), Wu and Curds (1979), Curds et al. (1983), Warren (1986), Foissner et al. (1991, 1992, 1994, 1995, 1999), Berger and Foissner (2003), Dovgal (2002), Jankowski (2007), etc.

For the comparative analysis of the ciliate communities, we used the Jaccard index (for soil ciliates), the Czekanowsky-Sørensen faunistic similarity coefficient (the faunistic commonality index) and, to assess diversity, the index of “genus saturation”, defined as the ratio of the number of species to the number of genera (Ochapkin et al., 2003).

The number of large ciliate species was calculated visually under a binocular microscope. For all other species, Goryaev camera was used. According to the parameter of frequency of occurrence in a water body, all detected species of ciliates were distributed according to the following classification: “very rarely” (< 5%), “rarely” (5–15%), “not often” (15–40%), “often” (40–60%), “very often” (60–80%),

“mass development” (> 80%) (Shkundina and Martynenkova, 2002).

The material was summarized using Small and Lynn’s taxonomic system (Small and Lynn, 1985, 2000; Lynn, 2008), taking into account recent changes in taxa names and the presence of significant taxonomic differences.

Results

A faunal survey of ciliate communities of natural and anthropogenic ecosystems of the southern Russian Far East revealed 307 species of ciliates. They belong to 2 subtypes, 11 classes, 32 orders, 77 families, and 124 genera. The most representative classes (by the number of species) were Oligohymenophorea (86 species), Spirotrichea (69), and Litostomatea (44). In total, these taxa comprised 65% of the overall species diversity of ciliated protist in the studied water bodies. The greatest number of species was recorded in the genera *Vorticella* (17), *Oxytricha* (10), *Stylonychia* (9), *Epistylis* (9), *Prorodon* (8). In addition, 59 species were identified only to the genus level, which corresponds to 19.2% of the total faunal richness of ciliates (Table 1).

The greatest species richness of ciliated protozoa was found in water bodies of the southern part of Sakhalin Island, Primorsky Krai, and in soils of Middle Priamurye, while the lowest – in the territory of Amur Oblast. In general, the diversity of ciliates in natural watercourses of Sakhalin and Khabarovsk turned out to be richer than in the surveyed water bodies of the respective regions. By comparing similar data between natural and anthropogenically transformed water bodies (aeration tanks), we

found that the ciliate community of wastewater treatment plants in Ussuriysk (Primorsky Krai) was significantly poorer than that of the Komarovka River in this region. In the Amur Region and Khabarovsk Territory, the number of ciliate species in natural and anthropogenic objects was approximately the same.

The faunistic similarity coefficient of the studied ciliates varied in a wide range: from 11.7% to 68.3%, with an average value of 31% (Table 2). The highest index of faunistic commonality was observed in ciliates of one geographic area: the southern part of Sakhalin Island (68.3%), water bodies-soils of the Amur Region (65.6%), and water bodies of the Khabarovsk Region (59.2%). When comparing similar data for individual territories, we found that the faunistic similarity coefficient between Sakhalin Island and Khabarovsk Krai was 36%, which, in turn, was the maximum value. In the pairs of Sakhalin Island – Primorsky Krai, and Primorsky Krai – Khabarovsk Krai, the values of the faunistic commonality index were 29.8% and 29.3%, respectively. The lowest faunistic similarity coefficient was found for Sakhalin Island – Amur Region (22.1%) and Primorsky Krai – Amur Region (23.6%).

A comparative analysis of ciliocenoses revealed that:

- the highest faunistic similarity in watercourses of the southern part of the Russian Far East was noted in the pair Sakhalin Island – Khabarovsk Krai (45.5%). Similar results were obtained for the lentic biocenoses of these geographical areas – 37.5%;

- for the aeration tanks of Ussuriysk and Khabarovsk wastewater treatment plants, the faunal commonality index was 42.2%;

- for soil ecosystems of the Amur Region and Khabarovsk Krai – 29.7%.

The study of ciliate communities allowed us to distinguish the following complexes of ciliates of the studied biocenoses.

I. The indicative complex represented by eurytopic species: *Vorticella convallaria* complex, *V. microstoma* complex, *V. campanula*, *Tachysoma pellicionellum*, *Aspidisca cicada*, *Trithigmostoma cucullus*, *Uronema marinum*, *Paramecium aurelia* complex, *Coleps hirtus*, *Chilodonella uncinatus*, and *Spirostomum teres*. Representatives of this group colonized almost all surveyed biotopes in the Russian Far East. According to literature data (Stout, 1955; Alekperov, 2012) and our observations, these species are tolerant to some vital abiotic environmental factors

(thermal regime, concentration of dissolved oxygen in water, pH).

II. The faunal complexes, in which organisms are confined to living in water or soil objects of just one geographic region. Those are the following complexes.

1. **The faunal complex of the Amur Region** included 17 species, three of which (*Paraureonema acutum*, *Chilodonella* sp., *Oxytricha* sp.) were recorded in all water bodies of this region. *Oxytricha* sp. was dominant in the storage pond and *Chilodonella* sp. – in the aerotank. Faunistic subcomplex of a natural water reservoir (Gashenka Lake) included five species: *Histiculus vorax*, *Strombidium nabranicum*, *Spathidium procerum*, *Vorticella communis*, and *Stylonychia* sp. In the storage pond, no stenotopic species were found. Aerotank subcomplex consisted of six species: *Kahliella costata*, *Acineta cuspidata*, *A. foetida*, *A. grandis*, *Epistylis urceolata*, and *Vorticella vernalis*. The subcomplex of brown forest soils included only *Trachelius ovum*, which was recorded by single findings. Four species of the Amur complex (*Oxytricha* sp., *Stylonychia* sp., *Chilodonella* sp., *Dysteria* sp.) were identified only to the genus level. *Strombidium marinum* and *Dysteria* sp. were found in two objects: Gashenka Lake and brown forest soils.

2. Of the 41 species in the **Primorsky complex**, five species (*Trachelolophos filum*, *Sphaerophrya pusilla*, *Tokophryella carchesii*, *Enchelys pupa*, and *Chilodonella* sp.) were registered both in the watercourse and in aeration tanks of wastewater treatment plants. The riverine subcomplex of ciliates was found only in the area of the Komarovka River, numbered 28 species, including *Trachelocerca tenuicollis*, *Blepharisma hyalinum*, *Condyllostoma* sp., *Stentor* sp., *Oxytricha* sp., *Stylonychia* sp., *Urostyla* sp., *Holosticha* sp., *Euplotes aediculatus*, *Euplotes* sp., *Strombidium mirabile*, *Strombidium* sp., *Rimostrombidium velox*, *Strombidium minus*, *Codonella* sp., *Tintinnidium semicillatum*, *Caenomorphia sapropelica*, *Lacrymaria coronata*, *Spathidium cithara*, *Paramecium* sp., *Leptopharynx euglenivorus*, *Prorodon niveus*, *Prorodon* sp., *Urotricha pusilla*, *Dexiotricha granulosa*, *Cyclidium heptatrichum*, *Pleuronema multinucleatum*, and *Epistylis anastatica*. The aerotank subcomplex included eight stenotopic species: *Metopus striatus*, *Brachonella spiralis*, *Amphileptus* sp., *Coleps elongatus*, *Carchesium epibioticum*, *Epistylis thienemanni*, *Zoothamnium parasiticum*, and *Opercularia minima*. A significant number of ciliate representatives in this complex (13 species) could not be identified to species level because they were found only once in the samples.

Table 2. The faunistic similarity coefficient of ciliated protozoa of the southern Russian Far East (according to the Czekanowsky- Sørensen formula, in %).

Water object		Sakhalin Island		Primorsky Krai		Amur Region			Khabarovsk Krai			
		Water bodies	Watercourse	Treatment facilities	Water body	Treatment facilities	Soils	Watercourses	Watercourses	Water body	Treatment facilities	Soils
Sakhalin Island	Watercourses		68.3	34.5	24.7	25	29	16	45.5	35.5	30.4	29.1
	Water bodies			30.6	29.6	22	25.6	15.2	47.9	37.5	34.9	29.7
Primorsky Krai	Watercourse				15.1	29.5	27.2	20.3	31	38	26.5	27.9
	Treatment facilities					20.4	30.7	13.5	28	21.7	42.2	19.3
Amur Region	Water body						49.3	65.6	34.6	36.5	18.1	34
	Treatment facilities							38.8	41.1	28.2	31.3	26
	Soils								26.6	23.5	11.7	29.7
Khabarovsk Krai	Watercourses									59.2	38.4	32.2
	Water body										33	27.3
	Treatment facilities											19.2
	Soils											

3. Of the 65 species of **the Sakhalin complex**, 27 species were found only in the subcomplex of watercourses and 12 species – only in small water bodies. In addition, 26 species were observed in all types of water basins of this region. Species such as *Steinia platystoma* (up to 600 ind./ml) and *Glaucoma scintillans* (up to 700 ind./ml) were abundant in late summer and early autumn in the Lyutoga, Krasnoselskaya, and Rogatka rivers; *Urozona butschlii* (up to 800 ind./ml) in summer and *Holophrya nigricans* (up to 125 ind./ml) in autumn were abundant in the Bezymyannaya water flow. At the same time, the frequency of occurrence of these species was rather low – from 8.4 to 18.9%. *Diaxonella pseudorubra* and *Glaucoma reniforme* were common (“not rare”) in some streams in summer and *Euplotes eurystomus* –

in autumn; *Sterkiella histriomuscorum* and *Plagiopyla nasuta* were regularly found in the samples from Bolshoi Lake in summer. The remaining 54 species in the samples were rare, of which 12 species (*Pseudo-blepharisma tenue*, *Climacostomum virens*, *Oxytricha aeruginosa*, *Aspidisca major*, *A. polypoda*, *Trachelophyllum apiculatum*, *Homalozoon vermiculare*, *Didinium nasutum*, *Cyclotrichium viride*, *Rhabdostyla inclinans*, *Hastatella radians*, and *Vorticella marginata*) were found in the samples just once. The number of species that could be determined only to the genus level here was low – only six (3.8%). Of them, four species (*Blepharisma* sp., *Euplotes* sp., *Caenomorphia* sp. and *Prorodon* sp. 1) were found in the subcomplex of watercourses, two species (*Prorodon* sp. 2 and *Rhabdostyla* sp.) – in small reservoirs.

4. **The ciliofauna of Khabarovsk Krai** included 72 species, of which seven species (*Stylonychia* sp., *Metopus* sp., *Podophrya fallax*, *Chilodonella* sp., *Rhabdostyla pyriformis*, *Paramecium* sp., and *Opercularia nutans*) were found in the subcomplex of watercourses. The frequency of occurrence of these species varied from «very rarely» to «often» (1.3 to 41.6%). Most of these species live in periphyton and benthos, and single cells of *R. pyriformis* were obtained from the body surface of freshwater crustaceans (Cyclopidae). A subcomplex of aeration tanks of wastewater treatment plants was represented by 15 species. The basis of the group consisted of representatives of Oligohymenophorea (genera: *Epistylis*, *Vorticella*, *Zoothamnium*, *Cothurnia*) and Suctoria (genera: *Acineta*, *Discophrya*, *Dendrosoma* etc.). In all seasons and at any anthropogenic loading, *Epistylis plicatilis* was a mass species, also *Epistylis chrysemidis* (61.6%) and *Vorticella nebulifera* (50%) were considered species with high frequency of occurrence. The overwhelming part of a faunal subcomplex of ciliates of wastewater treatment plants of Khabarovsk was presented by the species encountered “rarely” (*Epistylis longicaudatum*, *Discophrya elongata*, *Acineta tuberosa*, *Zoothamnium procerius*). In the soil subcomplex, 43 species in the Middle Priamurye were found. At the same time, the distribution and frequency of occurrence of ciliates were different for various biotopes. For example, *Espejoia musicola* and *Vorticella putrina* were found only in a fir-spruce forest, and *Amphileptus flexilis* — in a coniferous-broadleaf plant association. In the soils of Voronezh Heights, *Plagiocampa mutabilis* was among the dominant species, but *Dileptus gigas* and *Meseres cordiformis* were among the specific ones. *Codonella cratera* was specific in soil samples of Bolshekhetsirsky Reserve. The number of species that could be determined only to the genus level in this complex was 35, of which 28 species were found in soils of Khabarovsk Region.

In general, the greatest species richness of ciliated protozoa in most of the surveyed biotopes was observed in August-September. The core of the late summer fauna of ciliates in Khabarovsk watercourses were *Paramecium caudatum*, *Uronema marinum*, *Spirostomum teres*, and *Colpidium colpoda*. In spring and early autumn, the species richness was low (10–15 species). In a fir-spruce forest, 14 species of ciliated protozoa were identified in spring, 1.3 times more in summer, and 2 times more in autumn. Dominant species in the autumn season were *Tri-thigmostoma cucullus*, *Colpoda maupasi*, *C. steinii*,

Strombidium sp., *Aspidisca cicada*. The abundance of the above-mentioned species varied from 750 to 1,200 ind./g of soil in the autumn period. In spring, summer, and autumn, 23, 32, and 27 species were found in Gashchenka Lake (Amur region), and 20, 25, and 22 species of ciliates were recorded in brown forest soils in the same seasons, respectively.

Discussion

Before the start of the XXI century, no comprehensive studies of the ciliate population in the southern part of the Russian Far East have been conducted. The only work that combined information on the soil and freshwater ciliofauna of the Middle Amur region (Nikitina et al., 2011) is now somewhat outdated because of serious changes in Ciliophora taxonomy. In addition, significant expansion of the boundaries of the present study (if compared to the previous investigations) allowed us to register 131 previously unrecorded ciliate species. Such a large number of newly found species of ciliates in the area is due to several factors. Firstly, this fact can be explained by the pioneering information on the ciliate communities of the southern part of Sakhalin Island (65% of the total number of species not mentioned before) and Primorsky Krai (33%). Secondly, it is due to the revision of taxonomic positions and synonymic names of some ciliate protists (Aescht, 2001; Jankowski, 2007; Lynn, 2008). Thirdly, our field studies lasted longer than in the previous investigations. The above-mentioned circumstances prove the fact of insufficient study of the ciliocenoses of the researched region. The same conclusions were reached by the protistologists who investigated other biotopes. For example, V.V. Zharikov (2011) noted that 88 species of ciliates were found in the Volga basin by 1936, 190 species — by 1979 and by 2010 — over 500 species. Similar results were obtained by W. Foissner (2006), in whose opinion more than 50% of the species richness of protists were still undescribed by 2006. A. Chao et al. (2006) analyzed 359 soil samples collected from different continents; this analysis allowed recording in total 964 soil ciliate species (644 described and 320 undescribed).

We used available literature data on ciliate species diversity in different regions of Russia and beyond for a comparative zoogeographic analysis. The coefficient of faunistic similarity of ciliocenoses, grouped according to the origin of a water body (i.e.,

Table 3. The faunistic similarity coefficient of ciliates of the southern Russian Far East and other regions (according to the Czekanowsky-Sorensen formula, in %).

A) watercourses

Locations	Watercourses				
	Omsk Region	Tyumen Region	Miass River	Byk River	Volga River
Primorsky Krai	28.1	21.2	11.3	42.1	37.6
Sakhalin Island	34.1	27.3	17.7	37.3	35.5
Khabarovsk Krai	35.9	37.9	27.3	40.1	31.9

Note: Omsk Region – Achairka River, branch Pristan, and Shuchka Channel (Sinenko, 2014); Tyumen Region – Rivers Mergen, Karasyl, Ishim (Syppes, 2010); Miass River (Trofimova, 2010); Byk River (Chorik, 1968); Volga River (Zharikov, 1997).

B) water bodies

Locations	Water bodies				
	Omsk Region (south)	Omsk region (west)	Floodplain reservoirs of Samarskaya Luka	Water bodies of the Samarskaya Luka floodplain terrace	Karst lakes of Samarskaya Luka
Amur Region	41.1	31.3	17.1	18.8	18.2
Sakhalin Island	25.7	24.4	24.7	27.3	34
Khabarovsk Krai	31.6	23.9	25.8	29.8	32.8

Note: Omsk Region (south) - (Sinenko, 2014); Omsk region (west) (Miachina, 2010); Samarskaya Luka (Bykova, 2005).

C) treatment facilities

Locations	Treatment facilities			
	Settlements Hovsan and Sahil (Azerbaijan)	Wels (Austria)	England, Scotland	Borisoglebsk (Russia)
Khabarovsk	16.2	24.2	29.6	14.6
Svobodnyi	34.4	17.9	42.7	31.2
Ussuriisk	36.7	14.8	36	20.2

Note: Settlements Hovsan and Sahil (Mamedova, 2016); Wels (Oberschmidleitner and Aescht, 1996); Borisoglebsk (Sharapova, 2010); England, Scotland (Curds and Cockburn, 1970).

natural or anthropogenic), is presented in Table 3.

Thus, the highest values of the ciliocenoses commonality index in the studied river ecosystems (Table 3A) were observed in the Byk River (Chorik, 1968) (37.3-42.1%), and the lowest – in the Miass River (Trofimova, 2010) in pairs with the Komarovka River (11.3%) and the southern part of Sakhalin Island (17.7%). On average, the faunal similarity coefficient for the surveyed watercourses in Primorye was equal to 23.3%, in the southern part of Sakhalin Island – 25.3%, in Khabarovsk – 28.8%. When comparing lentic biocenoses by a similar parameter (Table 3B), high values of the species similarity were recorded between the Amur and Omsk (southern part) regions. For aeration

tanks (Table 3C), the maximum parameter of ciliate commonality was 42.7% between Svobodny and sewage treatment plants in England and Scotland (Curds and Cockburn, 1970). The lowest commonality index values were in pairs Khabarovsk – Borisoglebsk (Sharapova, 2010) and Ussuriisk – Wels (Oberschmidleitner and Aescht, 1996).

The faunal diversity of ciliates in natural biotopes was much richer than that in anthropogenic water bodies. The living conditions of ciliate in anthropogenic water bodies are not very diverse, which does not support high species richness (Curds, 1973; Foissner, 2016). Thus, the fact that the number of known ciliate species in aeration tanks is lower than in rivers and lakes is not accidental.

Nevertheless, W. Foissner (2016) suggested that the relatively low diversity of ciliated protozoa in wastewater treatment plants is due to the low number of studies in these habitats. However, the highest values of “genus saturation” were observed exactly in treatment plants (Primorye – 2.18; Amur Region – 1.9; Khabarovsk Territory – 1.69).

The coefficient of faunistic similarity of ciliates was generally low (Table 3), which is especially evident when comparing natural and anthropogenic (aeration tanks) biotopes. We infer that this fact was caused by the following factors: significant distance between water bodies; similar origin (i.e., natural or anthropogenic water bodies or flows) and/or belonging to the same river system; influence of some specific environmental factors. Thus, for sewage treatment plants in Ussuriysk, the coefficient of species similarity ranged from 13.5% to 29.6%, and for Khabarovsk – from 11.7 to 38.4%. In addition, 14% of specific species belonging mainly to the subclasses Suctorina (genera: *Acineta*, *Discophrya*, *Dendrosoma*, *Trichophrya*, etc.) and Peritrichia (genera: *Epistylis*, *Carchesium*, *Opercularia*, *Vorticella*, etc.) were recorded in the aeration tanks. The homogeneous environment created by humans in aeration tanks, as well as maintained aeration of the sludge mixture and constant water temperature, are important factors for colonization of the habitat by periphyton protistofauna. The frequency of occurrence of these species was low (usually not more than 15%). The reason for such low values is that they are stenobionts in relation to a number of environmental factors: concentration of dissolved oxygen in water and high hydrostatic pressure – for Suctorina, and the presence of currents for Peritrichia (Dovgal, 2001, 2002; Zhukov, 2012). P. Bartosova and E. Tirjakova (2008) showed that only 25% of described species have been recorded from soils and freshwater habitats.

The identified features of the seasonal dynamics of ciliated protozoa also matched the previously published results. For example, P. Zingel (2005) researched the seasonal dynamics of plankton ciliates in a hypertrophic Lake Verevi (Estonia). In the metalimnion of this lake, the ciliate abundance was maximal in August. The decline in ciliate numbers in the early summer coincided with a decline in zooplankton abundance, because the latter actively consumed ciliates. Similar results were reported from the Lake Vortsjarv (Estonia) (Zingel and Noges, 2010). Researchers found a recurrent trend in ciliate seasonal dynamics. The number of species and biomass of ciliates increased starting from May,

and their abundance peaked in the late summer. There was a positive correlation between ciliates and phyto- and bacterioplankton in the Lake Vortsjarv (Zingel and Noges, 2010).

It should be noted that the highest faunistic similarity values were recorded between water bodies of one river system and/or common origin (e.g., in the case of wastewater treatment plants). Thus, between the Amur River and its small tributaries (Krasnaya, Chernaya, and Berezovaya Rivers) the above coefficient ranges from 47 to 58%. For the Krasnoselskaya and Rogatka Rivers and Prigorodny brook – small tributaries of the Susui River – it varies from 64 to 77%. This indicates the relative constancy of the faunal composition of ciliates, as well as probably similar ecological conditions of the habitats in question. P. Madoni and S. Zangrossi (2005), who studied ciliate communities in the Taro River (Italy), obtained similar results. The high values of faunistic commonality index (61–63%) were obtained between communities of closely located stations. In addition, high values of the species commonality of ciliate communities (59.2%) were recorded between the Central City Pond and watercourses of Khabarovsk, which is explained by the fact that the pond is fed with water from the Amur River.

In soil habitats of the Middle Amur Region, the trends in the formation of ciliate communities (in terms of species composition) were similar. Thus, the closely spaced biotopes of coniferous-broadleaved and fir-spruce forests had the highest percentage of ciliate faunal identity – 0.55 (according to the Jaccard index). In addition, soils of the same type (brown forest-podzolized) are located beneath these habitats. On the contrary, between the flooded willow-vein association and oak-birch forest, the commonality index was minimal (0.28), which can be related to the fact that during flooding, typical aqueous forms of ciliates are captured in soils.

Among ecological factors influencing the distribution of soil ciliates, soil moisture, temperature, and height location of biotopes are of greatest importance (Li et al., 2010; Duran-Ramirez and Mayen-Estrada, 2022). I.K. Alekperov (2012) came to the same conclusions when calculating the above-indicated coefficient for communities of ciliates in water reservoirs of Azerbaijan. At the same time, the scientist noted that the total number of species in a water body was determined by a complex of environmental factors and was less dependent on the distance between water bodies (Alekperov, 2012). In additional, X. Shi et al. (2015) investigated the

Table 4. Frequency range of eurytopic ciliate complex in some water bodies of the southern Russian Far East (in %).

Species	Water basins of Khabarovsk and its territory	Watercourses of Sakhalin Island
<i>Aspidisca cicada</i>	46.1–100	3.9–12.5
<i>Vorticella convallaria</i> complex	8.7–86.4	8–36.4
<i>V. campanula</i>	11.3	0.9–6.8
<i>V. microstoma</i> complex	11.2–39	4.5–21.8
<i>Tachysoma pellionellum</i>	17–89.3	3.2–32.5
<i>Paramecium aurelia</i> complex	20.8–30.6	2.6–21.7
<i>Uronema marinum</i>	47.6–78.7	5.2–71.9
<i>Spirostomum teres</i>	55.6–83.3	6.3–24.5
<i>Chilodonella uncinatus</i>	13.3	14.8–66.1
<i>Trithigmostoma cucullus</i>	35.8–65.8	0.6–8.9
<i>Coleps hirtus</i>	34.2–86.7	3.1–21.7

relationship between the development of protozoan communities and different environmental factors in a sub-tropic urban wetland ecosystem southern China. Correlation analysis revealed that temporal variation in protozoan complexes was related to the changes of environmental parameters, especially water temperature, dissolved oxygen, chemical oxygen demand and nutrients.

However, the comparative zoogeographic analysis did not confirm our hypotheses on the high faunistic commonality of closely located and similar by origin (natural or anthropogenic) water bodies. This is explained by the fact that the studies conducted in other regions were carried out during different periods and were performed using different taxonomic systems. Often this leads to “disappearance” of not only some species but also entire families from the faunistic lists. In addition, most of the earlier works were carried out for a limited time, which allowed scientists to identify mostly eurybionts and widespread species (Chorik, 1968; Zharikov, 1997; Mamedova, 2016). Besides, usually the described ciliate communities are composed of several dominant species providing most to the total abundance and many sparse species contributing to the rest, depending on the effort, size and volume of the samples (Weisse, 2014). Thus, the combination of the above circumstances can affect the quantitative and qualitative estimates of faunal diversity of ciliated protozoa.

The structure of the eurytopic complex of ciliates turned out to be typical for some freshwater basins in Russia due to high plasticity of many ciliates. For example, according to E.V. Zhirnova (2006), *Vorticella convallaria* has the following

morphophysiological adaptations that help to adapt to changes in environmental factors: a broad peristome that promotes maximum capture of food, high reproduction rate, and the presence of a free-floating stage that allows dispersal in space with better habitat conditions. Other species of the eurytopic cluster (*Aspidisca cicada*, *Paramecium aurelia* complex, *Tachysoma pellionellum*, *Uronema marinum*, *Chilodonella uncinatus*, *Trithigmostoma cucullus*, etc.) can inhabit several ecological zones of a water body (most often benthos and periphyton), which is also an advantage over highly specialized forms (Burkovsky, 1984). However, the frequency of occurrence of these species more often varied in a very wide range (Table 4).

The low frequency of occurrence of many eurybiont species in Sakhalin watercourses attracts special attention. This is particularly evident in the case of low abundances of *Aspidisca cicada* and *Trithigmostoma cucullus*. We infer that the observed fact is caused by the presence of water current (up to 0.8–1.2 m/s) and almost complete absence of bottom sediments. According to O.P. Dubovskaya (2009), the formation of stable planktonic invertebrate communities is only possible at water current velocities below 0.25 m/s. *A. cicada* and *T. cucullus* spend most of their life cycle in active movement in the substrate searching for food. In the water midstream, they move inactively and cannot withstand a strong current (unlike large *Paramecium*, *Frontonia* or *Stylonychia*). Free-floating forms were found less frequently in the biotopes of sewage treatment plants compared to natural watercourses, while stalked *Vorticella convallaria* and *V. microstoma*, on the contrary, were rather common in the former. In

general, the core of ciliocenoses of the studied region is mostly represented by the species found “rarely” (5-15%) and “not often” (15-40%).

Conclusions

A large-scale faunistic study of ciliate communities in freshwater and soil biotopes of the southern part of the Russian Far East revealed 307 species of the ciliated protozoa. Species from the classes Oligohymenophorea (86 species), Spirotrichea (69), and Litostomatea (44) represented the basis (65%) of the fauna. The highest species richness of ciliates was observed in water bodies of southern Sakhalin, Primorsky Krai, and soil biotopes of Middle Priamurye. In general, the faunal composition of ciliate protists in natural biotopes was more diverse than that in anthropogenically transformed water bodies. In our opinion, this was due to the influence of human activity and low variability of environmental factors, since most of abiotic factors are artificially controlled in aeration tanks.

The coefficient of faunistic similarity of ciliate communities in the studied aquatic and soil biotopes varied in a very wide range (from 11.7 to 68.3%). At the same time, the highest coefficient values were noted between closely located objects of the same region (for example, in the case of southern Sakhalin and soils of Middle Priamurye), watercourses belonging to the same river system (in the case of rivers of Khabarovsk), and anthropogenic objects.

The complex of eurytopic ciliates included 11 species: *Vorticella convallaria* complex, *V. microstoma* complex, *V. campanula*, *Tachysoma pellionellum*, *Aspidisca cicada*, *Trithigmotoma cucullus*, *Uronema marinum*, *Paramecium aurelia* complex, *Coleps hirtus*, *Chilodonella uncinatus*, and *Spirostomum teres*. Despite their wide distribution, the frequency of occurrence of these species in water bodies varied considerably and was related to the effect of such factors as water flow, the presence of bottom sediments, and the specificity of cell locomotion. At the same time, highly specialized forms isolated from only one biotope represented the basis of ciliate fauna of the studied region. Separation of water and soil objects by geographic borders allowed us to distinguish four faunal complexes of ciliated protozoa. The richest were the Khabarovsk Krai (72 species) and Sakhalin (65) complexes.

The study demonstrated the need for further in-depth investigations of the species composition,

seasonal dynamics, and the trends in development of ciliate complexes in the Russian Far East.

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Supplementary material

Table S1. Taxonomy of ciliates of the southern part of the Russian Far East (Small and Lynn, 1985, 2000; Lynn, 2008)