Spatial distribution of nematode communities along the salinity gradient in the two estuaries of the Sea of Japan

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Summary. Spatial distribution and structure of nematode assemblages in two estuaries (long lowland Razdolnaya and mountain Sukhodol rivers, the Sea of Japan) were investigated. Sampling was conducted from freshwater to marine benthic habitats. The meiobenthic community was strongly dominated by nematodes. In both estuaries, the spatial distribution of nematode density, composition and feeding types related to the salinity gradient. From a total of 57 nematode species, 42 and 40 nematode species were identified in each estuary, respectively. The changes in the taxonomic structure of nematode fauna were found along the salinity gradient. Differences in nematodes community observed along each estuarine gradient were much lower than between the two estuaries. Only four species *Anoplostoma cuticularia*, *Axonolaimus seticaudatus*, *Cyatholaimus* sp. and *Parodontophora timmica*, were present in all sampling zones of both estuaries. Most of the recorded species were euryhaline, described previously in shallow coastal bays; only five freshwater species have been described previously from the freshwater habitat of Primorsky Krai.

Key words: community structure, euryhaline nematodes, free-living nematodes, Razdolnaya River estuary, Sukhodol River estuary.

Free-living nematodes are an important component of both marine and estuarine ecosystems (Giere, 2009; Mokievsky, 2009). It has been shown that nematodes play a leading role in the transformation of organic matter and the energy of desalinated ecosystems when there is a decrease in the proportion of macrobenthos in the total biomass of the benthic community (McLusky, 1981; Coull, 1999; Udalov *et al.*, 2005).

A 'critical' or 'barrier' zone within gradients of environmental parameters (the most important of which is salinity) is formed in the region when river and sea waters mix, and overcoming the most unfavourable zone requires a radical rearrangement of a number of physiological processes in aquatic organisms at a salinity of 5-8 practical salinity units (PSU), (alpha horohaline zone) (Starobogatov & Khlebovich, 1978; Khlebovich, 1989; Forster, 1998).

European and South-Eastern Asian estuaries have been studied in more detail than the North-Eastern Asian estuaries (Heip *et al.*, 1985; Soetaert *et al.*, 1995; Hua *et al.*, 2005; Adão *et al.*, 2009; Quang *et al.*, 2010; Quang & Nguyen, 2015; Thai *et al.*, 2018). The data of nematode and meiobenthic communities from the South-Eastern Russian region are available from several estuaries (Fadeeva, 2005; Shornikov & Zenina, 2014; Milovankina *et al.*, 2018). Nematode communities were described from marine parts of Peter the Great Bay and bays of seashores from the Sea of Japan (Fadeeva, 2005; Pavluyk *et al.*, 2007). However, data often are available only for marine or freshwater parts of an estuary; the information of nematodes in freshwater habitats is limited for Eastern Russian region.

The interests in estuarine zones are due to the potential possibility of the eutrophication of the Peter the Great Bay (Mikhaylik *et al.*, 2011). The purpose of the present study was to determine the structure and distribution of nematode assemblages in the two estuaries (long lowland Razdolnaya and mountain Sukhodol rivers, the Sea of Japan) and spatial distribution patterns of density and biomass, genera composition, and feeding types along the salinity gradient.

MATERIAL AND METHODS

The study was undertaken from May to September in 2010 and in July and September 2013 during the expedition of the research workers of

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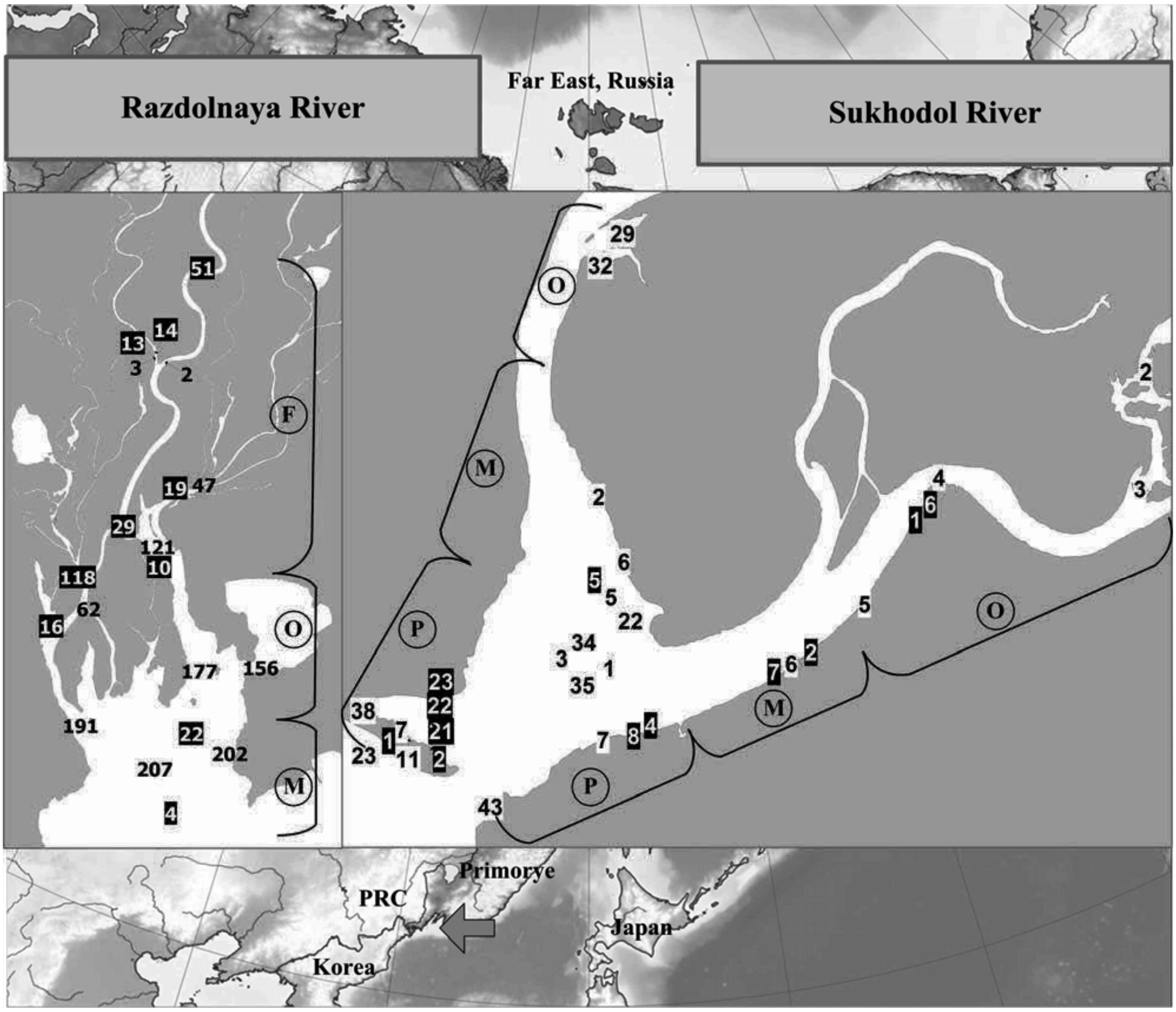

Fig. 1. Schematic map of samples areas with station numbers and salinity zones. The stations numbers without frame were in Razdolnaya (2014) and Sukhodol (2010), with black frame were in Razdolnaya (2013) and Sukhodol (2013). P – polyhaline, M – mesohaline, O – oligohaline, F – freshwater zones of estuaries.

KIRRAM TINRO-Centre in the Sukhodol River estuary (Ussuryi Bay) and in July and September 2013, 2014 at the Razdolnaya River estuary (Amursky Bay) (Fig. 1).

Stations in 2010-2014 years were selected in river zones and inner estuary and fully covered the salinity range. Stations were located at several hundred meters from each other and stations were chosen by sediment type and depth to be as similar as possible. Samples were collected at 53 stations from 0.1 to 2.1 m depth.

Samples of hydrochemical characteristics were selected for the study simultaneously with sediment samples. Data on salinity are published by Vazhova & Zuenko (2015). The temperature and salinity were measured by the oceanographic probe YSI-6600V2 (USA) during the expedition (Vazhova & Zuenko, 2015).

Study areas. The Sukhodol River (Kangauz) flows into the Sukhodol Bay (Ussuri Bay). The length of the river is 45 km and the water catchment area is 617 km^2. The length of the internal estuary is about 2 km. The maximum width of the river in the estuary area is 100 m; the average depth is 1.3 m. The sediments are silt, aleurite, psammite and pebbles, in the outer part, and psammite and pebbles in the internal estuary. This estuary is considered relatively undisturbed and free from industrial pollution.

Razdolnaya River is influenced by fresh and marine waters and has developed a salinity gradient. The anthropogenic impact from China and Russia can influence the meiobenthic distribution. Silt dominates the mouth of the river where sand, shells and gravel were present. The width of the duct is not more than 50 m, the depth of not more than 2.5 m (Mikhaylik *et al.*, 2011). In the investigated period on the Razdolnaya River, surface temperature was 24.1-26.7°C; in the bottom temperature was 20.9-25.5°C, and strong desalination and fresh water were found far into the Amursky Bay. During the summer period of rain floods, the water in the estuary is completely desalinated. The salinity at the surface is not more than 5.3 PSU. In the river fresh water dominated at 0-2 m, and only 10 km from the estuary salinity increased in the deepest places to 19.7 PSU.

The salinity zones in the Razdolnaya River estuary were: mesohaline at stations 22 (September 2013); 121, 156, 177, 191, 202 (July 2014); oligohaline at stations 10, 62, 118 (September 2013); 16 (July 2014); the stations with fresh waters were 13, 14, 19, 29, 51 (September 2013); 2, 3, 47 (July 2014). Sukhodol River estuary had three salinity zones: polyhaline at stations 5, 7 (July 2010); 1, 2 (lower part of estuary); 21, 22, 23 (September 2013); mesohaline stations 43 (May 2010); 6, 2 (June 2010 middle part of estuary); 32 (July 2010); 7, 11, 22 (August 2010); 4 (July 2013); 8, 5 (September 2013); oligohaline stations 29, 34, 35, 38 (May 2010); 3, 5, 6 (August 2010); 2 (July 2013 upper part of estuary); 6 (September 2013) (Fig. 1).

The subtidal meiobenthos were collected at each sampling station by forcing a sediment corer (inner diam. 4.6 cm) 4 cm into the sediment to depth of 2 m (often 0.3-0.5 m). The Petersen Grab was used when the depth was greater than 1 m (sampling area was 0.025 m^2).

All samples were preserved by 10% buffered formalin. In the laboratory, each sample was stained with 1% Rose Bengal and washed through sieves with 1000 μm and 32 μm mesh sizes. Nematode body volumes were estimated from length and maximum body width measurements obtained by video image analysis in AxioCam MRc5 (program Axio Vision). The calculations of weight and derived parameters of nematodes were obtained by applying biometric conversion factor (Feller & Warwick, 1988). Maps and pictures were made in program Map Info.

Data analysis. As measures for nematode diversity and evenness we calculated Margalef diversity index (d), Shannon-Wiener diversity (H'(log2)), Berger-Parker index (B), Simpson's Index (D) and Pielou evenness index (J'), Fisher's logarithmic α– index. This spectrum of diversity indices gives a clear representation of the influence of rare (lower order indices) and more common (higher order indices) species on diversity. All the data per site were presented as mean ± standard deviation. In order to correct for the size-dependency of diversity indices (Soetaert & Heip, 1990) and as a means of comparing with other studies, the indices were calibrated on 100 randomly chosen individuals as described in Soetaert & Heip (1990). The significant differences in the univariate measures between sampling stations were tested by the parametric test one-way ANOVA or the non-parametric Kruskal-Wallis test, Z-test, Mann-Whitney U test, the non-parametric Friedman test, Pearson's chi-squared test, and Tukey's honestly significant difference test; PERMANOVA (Permutational Multivariate Analysis of Variance) by Euclidean distances and Bray-Curtis dissimilarities; the similarity percentage analysis (SIMPER) utilised the software STATISTICA 10. To investigate trophic diversity of the nematode assemblages, the Index of Trophic Diversity (ITD) was calculated according to Heip *et al.* (1985).

RESULTS

The studied estuaries differed in origin, size, relief, hydrological regime and degree of connection with the sea (Fig. 1; Table 1). Physicochemical parameters measured along the salinity gradient in both estuaries are provided in Table 1.

The estuary of the Razdolnaya River is oligohaline, and the estuary of Sukhodol is polyhaline. Hydrochemical conditions gradually changed from the upper to the lower intertidal zone of the Sukhodol River estuary; in particular, salinity increased from 0.8 to 16.6 PSU during the sampling period. In the Razdolnaya River estuary the salinity did not exceed 5.0 PSU.

The sediments were mainly aleurite, small and medium psammite in the desalinated part of the Sukhodol estuary; in the outer estuary the sediment is dominated by coarse sand and pebbles. Overall, the Razdolnaya estuary had larger proportions of the aleurite and pelite sediments than the Sukhodol estuary.

In the polyhaline Sukhodol estuary, the nematode density varied from 5-3425 ind·10 cm^{-2} with average 537 ± 379 ind·10 cm^{-2}; biomass was from 0.001-1.162 μg·10 cm^{-2} with a mean of 0.1151 ± 0.1007 μg·10 cm^{-2}. In the oligohaline Razdolnaya estuary, the nematode density was between 45-1465 ind·10 cm^{-2} with a mean of 407 ± 309 ind·10 cm^{-2} and 676 ± 140 ind·10 cm^{-2} at July and 139 ± 27 ind·10 cm^{-2} at September; biomass values were

Table 1. Environmental variables in the Razdolnaya and Sukhodol estuaries.

River	Length, km	Catchment area, km ^{2}	Max wide, m	Average depth, m	Dominated type of sediments	Length of inner estuary, km	Salinity, PSU	Depth, m
Razdolnaya River	191	6820	200	2.0	Silt, aleurite, psammite	25	0-4.88	0.5-1.7
Sukhodol River	45	617	100	1.3	Silt, aleurite, psammite, pebble	2	0.2-18.64	0.2-0.3

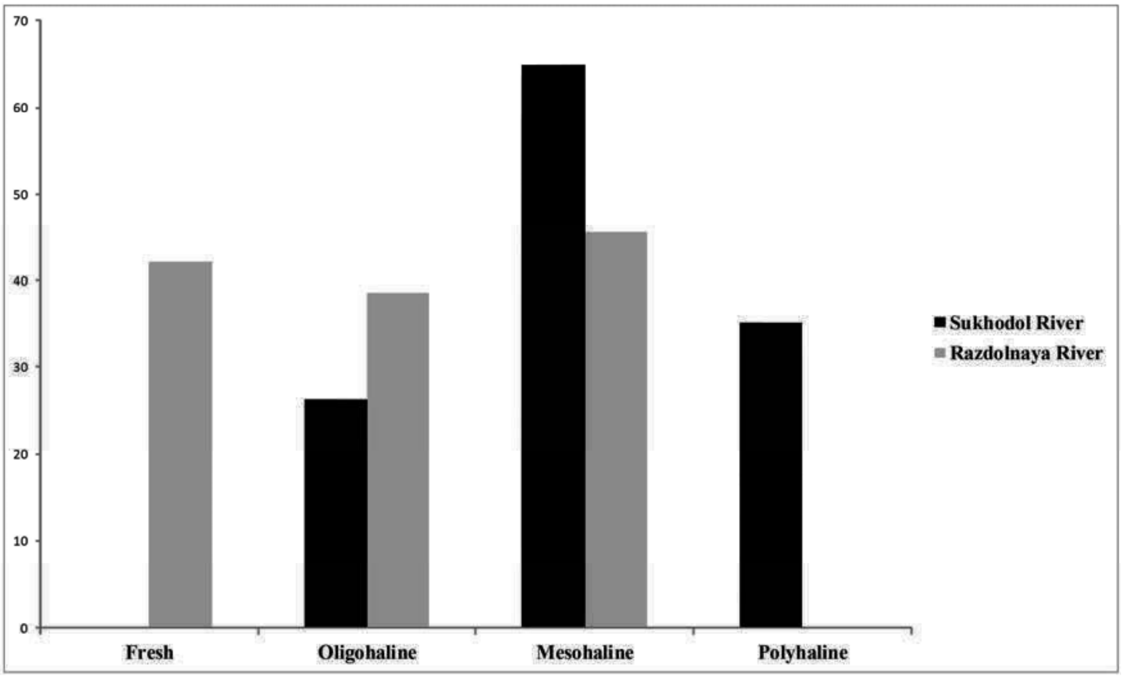

Fig. 2. The distribution of nematode species density of zones of salinity in the Sukhodol River and Razdolnaya River estuaries.

0.010-0.202 $\mu g \cdot 10\ cm^{-2}$ with a mean of 0.0014-0.033 $\mu g \cdot 10\ cm^{-2}$.

There were significant differences in nematode density found between stations by the Z-test ($Z = 0.04$, $\chi^2 = 9.54$, $P < 0.05$). In the Razdolnaya estuary, the mean nematode density was lower 7.5 ± 4.5 $ind \cdot 10\ cm^{-2}$ at the freshwater section (station 51) and 8 ± 3.2 $ind \cdot 10\ cm^{-2}$ at the euhaline zone (station 4). Similarly in the Sukhodol estuary, significant differences in nematode density recorded between stations ($Z = 2.41$, $\chi^2 = 2.45$, $P < 0.05$) were due to the occurrence of high values in a single station (station 7), and shows difference from two estuaries.

In general, although the mean nematode density was higher in the Sukhodol estuary (29.5 ± 18.1 $ind \cdot 10\ cm^{-2}$) compared to the Razdolnaya estuary (19.8 ± 10.5 $ind \cdot 10\ cm^{-2}$), the number of species present in each salinity range was higher in the Sukhodol estuary (Fig. 1; Table 2). A total of 57 nematode species were identified in the both estuaries. There were 40 free-living nematode species identified from the inner Razdolnaya River estuary, belonging to 34 genera and 18 families; at the Sukhodol River estuary 42 species, belonging to 35 genera and 16 families were identified.

The richest families were Oncholaimidae (8 species), Xyalidae (8 species), Chromadoridae (5 species) and Linhomoeidae (5 species). A complete list of the species identified and their densities at each sampling station in both estuaries is provided in Table 2. Only four species were the most widespread, *Anoplostoma cuticularia* Belogurov & Alekseev, 1977; *Axonolaimus seticaudatus* Platonova, 1971; *Cyatholaimus* sp. and *Parodontophora timmica*

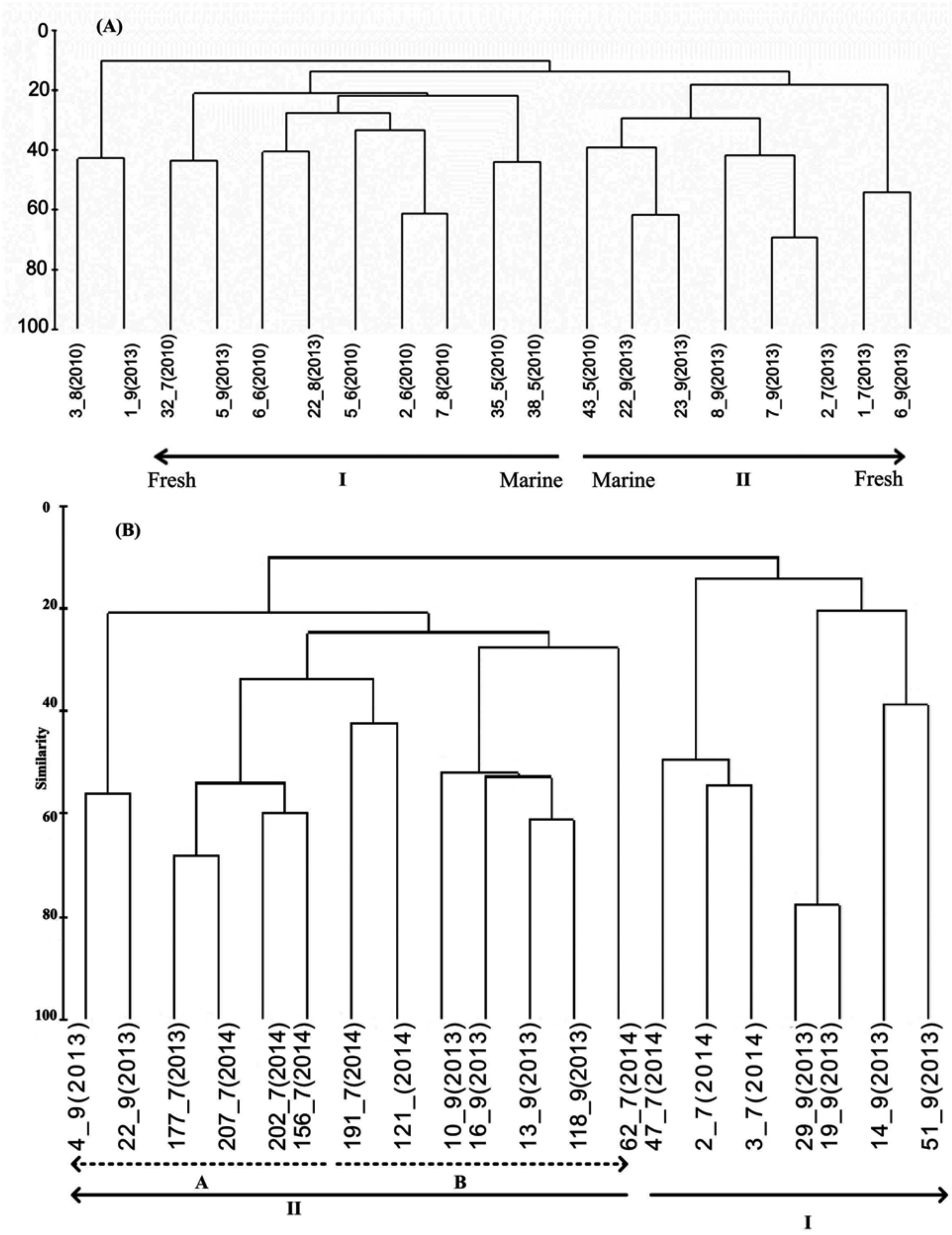

Fig. 3. Clusters for nematodes species density at Sukhodol River (A) and Razdolnaya River (B) estuaries by Bray-Curtis distance.

Pavlyuk & Belogurov, 1979 were present in all sampling zones in both estuaries.

The species richness in the community ranged from 1 to 15 species per sample in the Sukhodol estuary, and from 2 to 15 species per sample in the Razdolnaya estuary. The mean number of species in the sample was 6.8 ± 3.7 species per sample in the Sukhodol estuary and 6.3 ± 2.9 species per sample in the Razdolnaya estuary, but these values varied significantly from station to station.

Freshwater (7.5 ± 4.5 ind·10 cm^{-2}) and oligohaline (8.9 ± 6.2 ind·10 cm^{-2}) zones are characterised by the presence of freshwater taxa, low mean nematode density and diversity (15-20 genera). The freshwater species were Dorylaimidae gen. sp. 1, *Dorylaimus chassanicus*, *Daptonema inversum*, *Sphaerolaimus limosus*, *Theristus brevisetosus*, *Daptonema ecphygmaticum*, *Hofmaenneria gratiosa* and *Ironella* sp.

The mesohaline zone (16 stations) is characterised by high density and occurrence of several species such as *Hypodontolaimus ornatus*, *Admirandus multicavus*, *Cyatholaimus* sp., *Metalinhomoeus* sp., *Axonolaimus seticudatus*, *Parodontophora timmica* and *Daptonema setosum*. Mean density was 14.8 ± 7.65 ind·10 cm^{-2}.

The increase of salinity to 12.3-19 PSU (polyhaline zone) was registered in June in the Sukhodol River estuary with mean nematode density of 3.3 ± 2.6 ind·10 cm^{-2} and with euryhaline species *Anoplostoma cuticularia*, *Cyatholaimus* sp., *Hypodontolaimus ornatus*, *Halichoanolaimus* sp., *Neochromadora poecilosoma*, *Ironella* sp., *Sphaerolaimus limosus*, *Oncholaimium japonicum*, *Parodontophora timmica*, *Ptycholaimellus adocius* and *Terschellingia longicaudata*.

The cluster analyses were first calculated between data of species nematode density from Sukhodol and Razdolnaya estuaries. The analysis shows two groups of clusters and the first group comprised the Sukhodol River estuary stations. The taxocene of the estuarine zone is not distinguished by a specific set of species and consists of species characteristics of the nematode community of both desalinated and marine zones (Fig. 3).

There are differences between species composition and structure in the two estuaries; therefore, the cluster analyses were calculated separately for both estuaries. The cluster analysis reflected the spatial distribution of nematodes along the salinity gradients of the Razdolnaya and Sukhodol estuaries (Fig. 3).

The classification of Razdolnaya estuary species combination (Fig. 3) showed that all stations are quite clearly divided into two main groups (I and II) by the average abundance and species richness. The first group of stations occupies predominantly the aleurite pelite (*Md* – 0.51 mm, *Pl* – 79.4%) sediments and covers freshwater (< 0.5) biotopes of the of the lower part of the Razdolnaya River estuary (Fig. 3). Among the 24 nematode species that are found in this zone, only five are freshwater (*Dorylaimus chassanicus*, *Hofmaenneria gratiosa*, *Theristus brevisetosus*, and two species of the family Dorylaimidae). The effect on the density of this species assemblage is caused by representatives of the genus *Parodontophora* and *Tripyloides* sp., each with a high population density and *Leptolaimus* sp. (Table 2).

The stations of the second group are located in the inner part of the estuary at the border of river and brackish water sections in the sediments with the largest fine-silt fraction, which decreases towards the freshwater part (*Md* – 1.53 mm, *Pl* – 40-46%) and include oligohaline (0.5-5 PSU) estuary waters. From 22 species of free-living nematodes, only two are freshwater species, *Paraphanolaimus* sp. and Dorylaimidae gen. sp. 1 (Table 2). The local communities formed in this estuary zone and were represented by various combinations of marine and brackish water species that meet local conditions (primarily the salinity regime). The dominant species were *Hypodontolaimus ornatus*, *Parodontophora timmica* and *Daptonema setosum* (Table 2). In the mesohaline zone (II, B), the number of species increased to 26, including brackish-water and marine euryhaline species (*Oncholaimium japonicum*, *Anoplostoma cuticularia*, *Daptonema inversum*, preferring an average salinity of 4-8-10 PSU) but can withstand a gradual decline to 0 PSU, and rising to 15 PSU (in some seasons up to 18-20) (Milovankina *et al.*, 2018).

By species structure, this community is euryhaline, non-specific type, with a predominance of medium and small sized nematodes, common on sandy sediments of varying degrees of siltation. The typical interstitial forms are dominated by representatives of Monhysteridae (*Monhystrella* sp.) (Table 2). On the border of the freshwater and marine parts of the Razdolnaya River estuary, in the zone of extreme salinity fluctuations in summer (stations 4 and 22), *Sabatieria pulchra* were found, which are capable of penetrating deep into the sediment and adapting to anoxic conditions.

At the Sukhodol estuary, the cluster analysis revealed two distinct assemblages corresponding to two gradients. The gradients were clearly recognisable along the right and left arms of the river (Fig. 1). There is a gradient between assemblages from the freshwater section and those

Table 2. The SIMPER analysis results of species density in both river estuaries.

Taxon	Sukhodol River estuary		Razdolnaya River estuary	
	Contrib. %	Av. dissim.	Contrib. %	Av. dissim.
Hypodontolaimus ornatus Alekseev, 1970	9.43	9.95	5.9	6.47
Daptonema setosum Bütschli, 1874	7.57	7.99	2.63	2.89
Pseudoncholaimus venustus Belogurov, Belogurova & Leonova, 1972	6.69	7.06	–	–
Axonolaimus seticaudatus Platonova, 1971	6.45	6.81	0.84	0.93
Parodontophora timmica Pavlyuk & Belogurov, 1979	5.34	5.64	–	–
Anoplostoma cuticularia Belogurov & Alekseev, 1977	5.09	5.37	1.91	2.1
Neochromadora poecilosoma (de Man, 1893) Micoletzky, 1924	4.38	4.62	–	–
Daptonema ecphygmaticum (Wieser, 1959)	4.01	4.24	–	–
Oncholaimium japonicum Belogurov & Belogurova, 1981	3.64	3.84	1.01	1.11
Cyatholaimus sp.	3.4	3.59	–	–
Terschellingia longicaudata de Man, 1907	3.05	3.22	–	–
Nematoda unidentified	2.79	2.95	–	–
Pseudochromadora rossica Mordukhovich, Fadeeva, Semenchenko & Zograf, 2015	2.76	2.91	–	–
Eumorpholaimus sp.	2.66	2.81	1.39	1.52
Admirandus multicavus Belogurov & Belogurova, 1979	2.35	2.48	–	–
Parodontophora marisjaponici Platonova, 1971	2.05	2.16	11.4	12.51
Steineria copiosa Fadeeva, 1991	2.03	2.15	–	–
Ptycholaimellus adocius Dashchenko & Belogurov, 1984	2	2.11	–	–
Tripyloides sp.	1.81	1.91	4.49	4.93
Paracanthonchus sp.	1.63	1.72	2.43	2.67
Oxystomina elegans Platonova, 1971	1.56	1.65	–	–
Metachromadora itoi Kito, 1978	1.49	1.58	–	–
Sphaerolaimus gracilis de Man, 1876	1.46	1.54	2.11	2.31
Halichoanolaimus sp.	1.26	1.33	–	–
Monhystrella sp.	1.23	1.3	17.83	19.57
Chromadorita sp.	1.13	1.19	0.62	0.68
Parodontophora timmica Pavlyuk & Belogurov, 1979	–	–	20.78	22.81
Paralongicyatholaimus sp.	–	–	2.37	2.6
Theristus brevisetosus Alekseev, 1992	–	–	2.14	2.35
Viscosia stenostoma Platonova, 1971	–	–	1.72	1.89
Daptonema inversum Alekseev, 1984	–	–	1.28	1.41
Terschellingia longicaudata de Man, 1907	–	–	1.25	1.38
Ascolaimus sp.	–	–	1.2	1.32
Dorylaimus chassanicus Alekseev & Naumova, 1977	–	–	1.15	1.26
Megadesmolaimus rhodinus Tchesunov & Yushin, 1991	–	–	1.08	1.19
Desmodora sp.	–	–	0.66	0.72
Elzalia sp.	–	–	0.58	0.63
Hofmaenneria gratiosa Alekseev, 1983	–	–	0.51	0.56
Dorylaimidae gen. sp. 2	–	–	0.48	0.53
Polygastrophora sp.	–	–	0.47	0.52

Abbreviations: Contrib. % – the percentage of contribution of species similarity; Av. dissim. – Average dissimilarity.

from both the euhaline sections of the right river arm and left river arm. The first river arm is characterised by higher connection with the sea, the second is shallower.

The first cluster comprises stations from the left river arm and is characterised by highest densities of *Anoplostoma cuticularia* and *Cyatholaimus* sp.; the species *Hofmaenneria gratiosa*, *Neochromadora poecilosoma*, *Sphaerolaimus limosus* and *Terschellingia longicaudata* are found only in this cluster. The second cluster comprises stations from the right river arm with *Daptonema setosum*, *Paracanthonchus* sp., *Pseudochromadora rossica* and *Pseudoncholaimus venustus* only in this cluster, and with higher densities of *Hypodontolaimus ornatus*, *Parodontophora marisjaponici* and *Parodontophora timmica*.

The similarity percentage analysis (SIMPER) within which paired comparisons of sample groups were made, and the average contribution of each species to the average overall difference was determined with the Bray-Curtis coefficient. The combination of species, which gave differences between both estuaries with SIMPER, was represented by *Hypodontolaimus ornatus*, *Daptonema setosum*, *Pseudoncholaimus venustus*, *Axonolaimus seticudatus*, *Anoplostoma cuticularia*, *Parodontophora marisjaponici*, *Monhystrella* sp. and *Parodontophora timmica* (Table 2).

After analysis of the trophic structure in nematode communities, the results show domination of omnivores/predators and non-selective deposit feeders in the Razdolnaya estuary. The values of trophic diversity (ITD) indices are 0.79 and 0.86, respectively. The omnivores/predators and epistrate feeders were dominant in the Sukhodol estuary with ITD values of 0.71 and 0.64, respectively. In both estuaries the feeding strategy is typical for stressful conditions in assemblages. The taxonomic analysis of both rivers demonstrates the presence of regularity by species assemblages.

The Simpson's index, the Shannon diversity index and Berger-Parker index demonstrated that species assemblages are not similar in both rivers and also demonstrated low species diversity with low degree of differences in a community of both rivers. Fisher's index, the Margalef diversity index and Pielou evenness index show the small number of abundant species and the large proportion of uncommon species (Table 3). There are small differences between taxonomic indices in both estuaries, but equitability and evenness were slightly higher in the Sukhodol estuary and shows a greater degree of community sustainable.

By calculating a non-parametric Mann-Whitney U test for nematode species density, the values of sample comparison were from 104 to 295, which demonstrated low levels of similarity from samples. The highest significant differences were observed when comparing the oligohaline zone from the Razdolnaya and Sukhodol estuaries. The highest similarity was at the mesohaline zone of the two estuaries.

The non-parametric Friedman test with level of significance P = 0.026 and P = 0.037 with coefficient of Concordance Kendall = 0.84 and Average rank correlations r = 0.77, with χ^2 = 12.7 and χ^2 = 5.3 demonstrated a significant difference between samples. The Kruskal-Wallis one-way analysis of variance by ranks with P = 0.6 and with values = –167.2 and –192 showed differences between samples. Pearson's chi-squared test with level of significance P = 0.37 showed the highest coincidences by comparing mesohaline zones of Razdolnaya and Sukhodol estuaries. The application of Tukey's honestly significant difference test showed difference in means and that the data do not belong to one general sample with P = 0.099. PERMANOVA by Euclidean distances for salinity and sediment characteristics with F = 4.072 and P = 0.0819, F = 0.3982 and P = 0.7889 and by Bray-Curtis index with F = 1.362 and P = 0.0001, F = 1.009 and P = 0.4174 demonstrated that the two parameters contributed to permutation, dispersion and differences between stations in salinity zones and both estuaries. The results showed degrees of dissimilarity in structure of species composition at both rivers.

DISCUSSION

The most studied estuarine ecosystems for composition and distribution of meiobenthos and free-living nematodes are European (Smol *et al.*, 1994; Soetaert *et al.*, 1995; Udalov *et al.*, 2005; Adão *et al.*, 2009). Only the nematofauna of the Amur River estuary and Razdolnaya River estuary of the largest estuaries of the Russian Far East have been thoroughly investigated (Fadeeva, 2005; Pavlyuk *et al.*, 2007; Mordukhovich & Fadeeva, 2009; Milovankina *et al.*, 2018). The comparison of our results with published data shows that the density of the meiobenthos in the estuary is comparable to that of many tidal estuaries in Europe (Warwick & Gee, 1984; Heip *et al.*, 1985; Smol *et al.*, 1994; Soetaert *et al.*, 1995; Udalov *et al.*, 2005; Adão *et al.*, 2009), South-East Asia (Hua *et al.*, 2005; Quang *et al.*, 2010); North America and Australia

Table 3. The mean values with standard error of taxonomic and diversity indices for both estuaries.

Index	Mean values ± standard error	
	Sukhodol	Razdolnaya
Simpson's index (D)	0.65 ± 0.2	0.6 ± 0.1
The Shannon diversity index (H)	1.39 ± 0.4	1.25 ± 0.4
The Margalef (d) diversity index	1.24 ± 0.4	1.39 ± 0.5
Pielou evenness index (J')	0.81 ± 0.1	0.72 ± 0.2
Fisher's logarithmic α– index	1.7 ± 0.6	2.06 ± 0.8
Berger-Parker index (B)	0.46 ± 0.2	0.51 ± 0.2

(Tietjen, 1969; Nicholas *et al.*, 1992; Coull, 1999), although much lower than the maximum values of 14000-22000 ind·10 cm^{-2} (Smol *et al.*, 1994; Soetaert *et al.*, 1995; Udalov *et al.*, 2005; Mordukhovich & Fadeeva, 2009; Adão *et al.*, 2009).

Nematodes are resistant to changes of salinity using thick cuticles and effective osmoregulation (Capstick, 1959). In some cases, the salinity is an important ecological factor for distribution of meiofauna (Udalov *et al.*, 2004). The meiobenthic distribution can depend on fluctuations of salinity and the sum of other factors individually and their combinations (Giere, 2009). Many meiobenthic investigations show either the absence of any directed changes associated with salinity (Capstick, 1959; Warwick & Gee, 1984; Austen & Warwick, 1989), or a significant increase in density and biomass in the freshwater zone, or a decrease in these indicators by decrease in salinity (Gerlach, 1953; Bouwman, 1983; Fadeeva, 2005; Udalov *et al.*, 2005; Mordukhovich & Fadeeva, 2009; Wilson & Fleeger, 2013).

The meiobenthic density and biomass followed a pattern along the estuarine gradients in the lowland long, oligohaline Razdolnaya River, and in the fast mountain polyhaline Sukhodol River. The conditions were different in metric scale and time scale, and there were differences between estuaries and their conditions with environmental heterogeneity. The conditions were very heterogeneous in sampling stations, depth, season and tidal activity, and showed significant effect of factors and conditions in differences between nematode community structures. In general, the spatial distribution of subtidal nematode density and composition reflects both the sediment composition and the hydrodynamic conditions. The spatial distribution of nematodes depends on a combination of conditions: structure of sediments, hydrodynamics, anthropogenic pressure, values of salinity gradients, the presence of plants and temperature.

Our results indicate that differences in nematode communities observed along each estuarine gradient were much lower than between the two estuaries. A typical gradient of estuarine sediments was observed in the Razdolnaya estuary, with fractions of silt and clay increasing from the upstream sections towards the mouth of the estuary (Milovankina *et al.*, 2018). The water in the estuary is completely desalinated during the period of rain floods in summer. The estuary is characterised by significant inputs from anthropogenic activities (Vazhova *et al.*, 2011). In the Sukhodol estuary, where two arms of river (left and right) flow together, salinity has more pronounced fluctuations, with water changes during the spring-summer months from oligohaline (May) to polyhaline (June) to mesohaline (July, August). The right arm of the river is shallower (depth 0.2 m), with a smaller freshwater discharge; the left arm is deeper, and salinity tends to be higher than in the right arm during high-water periods.

In general, meiobenthic organisms predominated on silty sediments of the estuary with a high quantity of organic matter. Moreover, in the desalinated region, where the percentage of aleuropelite is higher, the total density of the meiobenthic organisms (eumeiobenthos and invertebrate larvae) was higher at some stations. In both estuaries, the spatial distribution of nematode density, composition, and feeding types appeared to be related clearly to the salinity gradient. On the other hand, nematode density was lower than in intertidal sediments, which are often more diverse (Soetaert *et al.*, 1994, 1995; Steyaert *et al.*, 2003). The genera *Anoplostoma*, *Metachromadora*, *Daptonema*, *Sphaerolaimus* and *Terschellingia* were also typical in the North and South European estuaries. Communities can occur in oligo-meso-poly-euhaline and freshwater habitats (Soetaert *et al.*, 1995; Adão *et al.*, 2009).

Most of the recorded species were euryhaline, previously described from coastal bays with low depth (Fadeeva, 2005; Pavlyuk *et al.*, 2007). Of the nematode species found in freshwater part of estuaries, only five are recognised as freshwater species (*Dorylaimus chassanicus*, *Hofmaenneria gratiosa*, *Theristus brevisetosus* and two species of the Dorylaimidae family) and have been described previously from the freshwater habitat of Primorsky Krai (Alekseev & Naumova, 1977; Alekseev, 1983, 1992). Probably, the fauna of freshwater free-living nematodes of Razdolnaya and Sukhodol rivers is not limited to the recorded species.

The maximum values of nematode density were recorded in the middle part of the estuaries. The maximum values of biomass were in shallow depths (0.5 m), near the water edge with salinity of 9 PSU. The maximum and minimum densities and species richness are not correlated with their location, but are often located in upper (fresh) or inner (marine) part of estuary. The species communities are characterised by the domination of 1-2 species, with adaptations for certain conditions (Figs 1 & 2; Tables 1 & 2). Both estuaries are similar in the composition of genera and families, but show marked differences in species composition; this may be explained by salinity changes and the presence of many ecological niches (Moens *et al.*, 1999; Fukami, 2015).

The genera *Axonolaimus*, *Chromadorita* and *Hypodontolaimus* were present at the river Sukhodol and Razdolnaya estuaries. These genera are typical for estuaries at higher latitudes. By contrast, the genera *Parodontophora* and *Desmodora* were recorded in the present work and they are typical for estuaries at lower latitudes (Fonseca & Netto, 2015). *Daptonema* and *Terschellingia* were also found in Asian estuaries (Hua *et al.*, 2005; Mordukhovich & Fadeeva, 2009). *Theristus*, *Sabatieria*, *Daptonema* and *Terschellingia* are the most common genera in estuaries worldwide. Plants and their roots were present in the investigated estuaries; the genera *Parodontophora*, *Desmodora* and *Terschellingia* are typical for estuaries with mangrove (Fonseca & Netto, 2015). These genera were found at some stations with plants and their roots at Razdolnaya and Sukhodol rivers. The most widespread species are *Parodontophora timmica*, *Hypodontolaimus ornatus*, *Anoplostoma cuticularia*, *Sphaerolaimus gracilis* and *Terschellingia longicaudata*.

The euryhaline genera *Daptonema*, *Oncholaimium*, *Oncholaimus*, *Parodontophora* and families Monhysteridae and Xyalidae were recorded. The Dorylaimidae is a true fresh water family, having been described from freshwater habitats, and its presence can indicate temporary fresh water areas. The species *Tripyloides* sp., *Viscosia stenostoma*, *Steineria copiosa*, *Admirandus multicavus*, *Daptonema inversum*, *Ptycholaimellus adocius*, *Desmodora* sp., *Cyatholaimus* sp., *Neochromadora poecilosoma* and *Daptonema setosum* were major contributors to the differences between the two rivers (Table 2).

The differences between feeding types and trophic structure of the nematode communities in the investigated estuaries demonstrated a combination of conditions typical for a defined estuary. The availability of trophic resources, organic matter, and other factors are also typical for world estuaries with different sediments types and amounts of organic matter (Moens & Vinx, 1997; Hodda, 2007; Dos Santos *et al.*, 2008; Adão, 2009).

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Милованкина А.А. и Н.П. Фадеева. Пространственное распределение сообществ нематод вдоль градиента солености в двух эстуариях Японского моря.

Резюме. Исследованы пространственное распределение и структура сообществ нематод в двух эстуариях (длинной равнинной реки Раздольная и горной Суходол). Отбор проб проводился от пресноводных до морских донных местообитаний. Мейобентосные сообщества характеризуются значительным доминированием нематод. В обоих эстуариях пространственное распределение плотности поселения, состава и типов питания нематод связано с градиентом солености. Из 57 видов нематод 42 и 40 видов нематод были представлены в обоих эстуариях, соответственно. Изменения таксономической структуры нематофауны обнаружены вдоль градиента солености. Различия в сообществе нематод, наблюдаемые вдоль каждого эстуарного градиента, были значительно ниже, чем между двумя эстуариями. Только четыре вида – *Anoplostoma cuticularia*, *Axonolaimus seticaudatus*, *Cyatholaimus* sp., *Parodontophora timmica*, – были представлены во всех зонах отбора проб обоих эстуариев. Большая часть зарегистрированных видов была эвригалинной, описанных ранее в прибрежных бухтах с небольшой глубиной, только пять пресноводных видов ранее были описаны из пресноводных местообитаний Приморского края.