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Marine nematode associations from an intertidal estuarine biotope

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Summary. Correlations between the 20 most prevalent marine nematode species from an intertidal estuarine biotope and sedimentary ecological factors yielded few significant relationships. Seven of the 20 nematode species were significantly correlated with distance from a pollution source, although few nematode species were correlated with concentrations of six different heavy metals and organic C. Sediment particle size was significantly correlated with only three species suggesting that as a single factor it had little impact on nematode distributions. The chi-squared test for contingency that tests the joint occurrences between species and indicates the statistical significance of their relationships was applied to the same 20 nematode species. Species abundance data were also analysed to determine whether any correlations existed between species. Many species in this study were significantly associated or correlated with each other. This contrasted with previous studies that reported nematode species from both deep-sea and estuarine biotopes were negatively associated.

Key words: associations, estuarine, intertidal, spatial distribution.

Many investigations have related salinity (*e.g.* Warwick, 1971; Jensen, 1984), sediment type (Ward, 1975; Soetaert *et al.*, 1995), pollution (Tietjen, 1977; Lambshead, 1986), location within an estuary (Alongi, 1987; Nicholas *et al.*, 1991), vertical distribution (Tietjen, 1969) and horizontal distribution (Neilson *et al.*, 1993) to species abundance and biodiversity within marine nematode communities. A few studies describe species complexes that are usually indicative of habitat (Warwick, 1971; Vanreusel, 1990).

However, there is a paucity of studies that investigate direct associations amongst nematodes at the species level. Typically samples are taken kilometres apart, along rivers (Moore, 1987), across estuaries (Bouwman, 1983) or from different estuaries (Soetaert *et al.*, 1995). Consequently, due to differing sedimentary ecological factors, samples have consisted of different nematode species (Soetaert *et al.*, 1995), thus, comparison of individual species within a given habitat between samples has not been possible.

Sediment granulometry has been shown to be one of the major environmental factors influencing nematode distribution in the marine environment (Warwick, 1971; Tietjen, 1980; Heip *et al.*, 1985; Vanreusel, 1990). Conversely, after analyzing 17 standardized marine nematode data sets from a range of disparate biotopes, Boucher and Lambshead (1995) suggested that sediment type on its own did not affect diversity.

Using data derived from a large number of samples taken from a relatively small area (maximum distance between samples 600m), the purpose of this present study was to determine the occurrence of direct associations amongst marine nematodes at the species level and relate them to sedimentary ecological factors.

MATERIAL AND METHODS

Samples were taken from around a short-fall sewage outlet in Invergowrie Bay (56°27'N 03°03'W), an intertidal area of the Tay Estuary, Scotland (Neilson *et al.*, 1993) which flows in an easterly direction. A total of 88 sediment samples were taken from several transects radiating out in Northeast, East, Southeast, South, West and Northwest directions (it was unsafe to take samples from a southwesterly direction) from the mouth of the sewage outlet, of which 87 were analysed. Along the Northwest and Southeast transects three replicate samples were collected at each of ten sampling stations located at 25 m intervals to 175 m and 225, 275 and 325 m from the sewage outlet. Single samples were taken from the remaining four transects at sampling stations located at 50 m intervals commencing 25 m and finishing at 325 m from the sewage outlet. Maximum distance between any two samples was 650 m.

Sediment samples were taken by means of a corer of 5cm internal diameter to a depth of 5 cm. The corer had a tapered rim to minimize boundary compression of the sample when inserted gently into the sediment. Samples were immediately placed in thick gauge polythene bags, to which 4% formalin was added. On return to the laboratory, samples were transferred to glass jars and more 4% formalin was added.

Nematodes were extracted from 20 cm^{-3} of sediment using the technique described in Neilson *et al.* (1996). Using low-powered microscopy, the first 200 nematodes encountered were hand-picked and transferred to 0.5 % glycerol. Thereafter, over a three-week period, nematodes were transferred into solutions of increasing glycerol concentration. After a few days in 100 % glycerol, nematodes were mounted on slides in a few drops of 100 % anhydrous glycerol. Seventy-five nematode species were identified, but many species were found only in a few samples that precluded them from meaningful statistical analysis. Therefore, only those species that occurred in a minimum of 50 % of the samples were included in the study.

Sediment analysis was determined using the method described by Buller and McManus (1979). Amounts of organic carbon were determined by weight loss after ignition at 480 °C for 12 h. Heavy metal (Cd, Cr, Cu, Ni, Pb, Zn) concentrations were obtained as follows: 30 g samples of sediment were acid digested with 6M Hydrochloric and 6M Nitric acids, followed by washing with 2M Hydrochloric acid to a final volume of 50 ml. The extractant was divided into two replicate 25 ml samples and analyzed using an ARL3510 ICP spectrometer (ARL Ltd Crawley, UK) and compared against known standards.

The statistical program Genstat 5 (Payne *et al.* 1987) was used for calculation of correlations between sedimentary ecological factors with nematode species abundance data and correlations amongst nematode species and also for a chi-squared test for contingency to determine significance levels of joint occurrences of the species.

RESULTS

Only 15 correlations (representing < 10 % of the total) between the abundance of the 20 most prevalent nematode species and measured sedimentary ecological factors were statistically significant (Table 1). Of these, seven were associated with distance from a pollution source with *Calomicrolaimus honestus* (De Man, 1922), *Daptonema procerum* (Gerlach, 1951), *Halalaimus gracilis* De Man, 1888, *Ptycholaimellus ponticus* Cobb, 1920 being positively correlated ($p < 0.05$; *P. ponticus* $p < 0.01$), conversely *Desmolaimus zeelandicus* De Man, 1880, *Dichromadora cephalata* (Steiner, 1916) and *Leptolaimus papilliger* De Man, 1876 were negatively correlated ($p < 0.05$) with distance from the sewage pipe (Table 1). Significant correlations ($p < 0.05$) with sediment particle size existed for only three species, *Anoplostoma viviparum* (Bastian, 1865), *L. papilliger* and *P. ponticus* (Table 1). The heavy metals Chromium and Nickel were all positively correlated with *P. ponticus*, whereas, Copper was positively correlated with both *H. gracilis* ($p < 0.05$) and *Sphaerolaimus balticus* Schneider, 1906 ($p < 0.001$)(Table 1).

The presence of any one species in a sample varied between 44 for *Paracanthoncus* sp. A. Micoletzky, 1924 and *S. balticus* and 87 for *A. viviparum*, *D. zeelandicus* and *L. papilliger* (Table 2). Therefore, the percentage of expected joint occurrences varied greatly between the studied species *e.g.* 39% of samples containing *Daptonema setosum* (Butschli, 1874) also contained *H. gracilis* whilst 50% of samples that contained *H. gracilis* also had *D. setosum*.

Correlations between species compared the relative abundance of one species to another. The majority of correlations were positive (Table 3). A positive correlation indicated a greater abundance of one species in the presence of another *e.g. A. viviparum* with *D. procerum* (Table 3). In contrast, a negative correlation indicated a decrease in abundance in the presence of another species *e.g. D. zeelandicus* and *Chromadorita nana* Lorenzen, 1973 (Table 3). The majority of nematode species were positively correlated with one another. There were only five negative correlations in total that were statistically significant. In contrast, there were 84 statistically significant positive correlations between species (21 correlations $p < 0.01$ and 46 correlations $p < 0.001$). Numbers of significant correlations for each species varied from two (both negative) for *D. setosum* to 15 (all positive) for *A. viviparum*.

The chi-squared test for contingency (Table 4) tested the joint occurrences between species and indicated the statistical significance of the relationships between species. The affinity of species

Table 1. Linear correlation coefficients between heavy metal content, organic carbon, median particle size and distance from a pollution source with the abundance of the 20 most prevalent nematode species; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Nematode species[1]	Cd	Cr	Cu	Ni	Pb	Zn	C	Median particle size	Distance from sewage pipe
Av	-0.220	0.196	0.260	0.178	-0.034	-0.077	0.211	-0.388*	0.331
Dz	-0.166	0.187	0.105	0.206	-0.048	-0.004	0.210	-0.061	-0.430*
Dic	0.007	0.187	0.271	0.151	0.146	0.158	0.143	0.163	-0.420*
Pp	-0.136	0.466**	0.329	0.514**	0.050	0.089	0.391*	-0.413*	0.551**
Ct	-0.231	-0.358	-0.126	-0.328	-0.243	-0.331	-0.345	-0.182	0.212
Lp	-0.130	-0.009	-0.115	-0.013	-0.120	-0.021	0.125	0.475*	-0.472*
Dpt	-0.182	0.206	0.014	0.200	-0.118	0.003	0.366	-0.359	0.181
Pc	0.007	0.182	0.104	0.267	0.063	0.066	0.141	-0.229	-0.073
Dpa	-0.173	-0.032	-0.007	-0.048	-0.124	-0.143	0.082	-0.097	0.078
Cha	-0.173	-0.091	0.085	-0.039	-0.074	-0.176	-0.044	-0.157	0.239
Dpp	-0.153	0.057	0.009	0.073	-0.102	-0.100	0.068	-0.368	0.432*
Cah	-0.130	0.023	-0.115	0.096	-0.142	-0.111	0.030	-0.283	0.389*
Pa	-0.146	0.186	0.067	0.217	-0.057	-0.048	0.252	-0.352	0.193
Dps	-0.194	-0.253	-0.283	-0.207	-0.259	-0.275	-0.202	-0.270	0.253
Dig	-0.169	0.220	0.293	0.247	0.023	-0.059	0.151	-0.291	0.375
Eb	-0.146	0.169	0.375	0.147	0.060	-0.020	0.116	-0.007	0.327
Hg	-0.105	0.274	0.458*	0.279	0.127	0.038	0.148	-0.203	0.494*
Sb	-0.124	0.367	0.672***	0.313	0.198	0.043	0.153	-0.067	0.288
Tp	-0.146	-0.360	-0.134	-0.319	-0.185	-0.281	-0.287	0.182	0.354
Cn	-0.096	-0.330	-0.153	-0.319	-0.167	-0.234	-0.373	0.087	0.097

[1]Av, *Anoplostoma viviparum*; Dz, *Desmolaimus zeelandicus*; Dic, *Dichromadora cephalata*; Pp, *Ptycholaimus ponticus*; Ct, *Chromadorita tentabunda*; Lp, *Leptolaimus papilliger*; Dpt, *Daptonema tenuispiculum*; Pc, *Paracanthonchus caecus* Micoletzky, 1924; Dpa, *Daptonema* sp. A.; Cha, *Chromadorina* sp.A Filipjev, 1918.; Dpp, *Daptonema procerum*; Cah, *Calomicrolaimus honestus*; Pa, *Paracanthonchus* sp. A.; Dps, *Daptonema setosum*; Dig, *Dichromadora geophila* (De Man, 1876); Eb, *Enoplus brevis*; Hg, *Halalaimus gracilis*; Sb, *Sphaerolaimus balticus*; Tp, *Theristus pertenuis*; Cn, *Chromadorita nana.*

within a genus varied. Species of *Dichromadora*, *Chromadorita* and *Paracanthonchus* did not show significant affinity for species from within its own genus. However, three species of *Daptonema*, namely, *Daptonema* sp.A. Cobb, 1920, *D. tenuispiculum* (Ditlevsen, 1918) and *D. procerum* showed a high degree of affinity for each other (generally $p < 0.001$). In contrast, these three *Daptonema* species were all negatively associated (generally $p < 0.01$) with *D. setosum.* Overall, six of the seven negative relationships that existed between species involved *D. setosum.* The specialized predators, *Enoplus brevis* Bastian, 1865 and *S. balticus*, had a few positive associations between species but had no negative relationships with any of the studied species. *Ptycholaimus ponticus* and *H. gracilis* had the highest number of significant positive relationships with other species, eight and nine respectively. Whereas, *D. cephalata*, *Chromadorita tentabunda* (De Man, 1890), *C. nana* and *Theristus pertenuis* Bresslau & Stekhoven, 1935 combined had only two significant negative associations.

DISCUSSION

Sediment particle size was significantly correlated with only three of the 20 most prevalent nematode species from this study suggesting that as a single factor it had little impact on nematode distributions. This is in contrast to previous studies that have reported sediment particle size to be a major environmental factor impacting on nematode distributions (Warwick, 1971; Tietjen, 1980; Heip *et al.*, 1985; Vanreusel, 1990), although Boucher and Lambshead (1995) suggested that sediment type on its own did not affect nematode diversity but other "local ecological factors" were contributory. Salinity was unlikely to be a limiting factor in this study, as salinity varies tidally at the site from 0.2 to 21 (Khayrallah & Jones 1975). Furthermore, the majority of the species studied had salinity tolerances within this range (Heip *et al.* 1985), and for many species Soetaert *et al.* (1995) suggested even higher levels of salinity tolerance, thus, differences in intensity and abun-

Table 2. Percentage joint occurrences of the 20 most prevalent nematode species. (Each row represents the percentage occurrence of a species in the number of samples positive for the 'column' species, *e.g.* of the 59 samples positive for *Daptonema setosum* (Dps), 39% had *Halalaimus gracilis* (Hg)).

	Av	Dz	Dic	Pp	Ct	Lp	Dpt	Pc	Dpa	Cha	Dpp	Cah	Pa	Dps	Dig	Eb	Hg	Sb	Tp	Cn
Av		100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Dz	100		100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Dic	100	100		93	91	100	93	90	92	93	95	91	87	91	91	90	91	93	92	87
Pp	100	100	73		70	100	80	77	76	77	86	84	89	78	73	74	91	79	63	69
Ct	100	100	96	95		100	100	96	96	96	95	98	93	98	96	98	94	98	98	95
Lp	100	100	100	100	100		100	100	100	100	100	100	100	100	100	100	100	100	100	100
Dpt	100	100	70	77	69	100		73	75	71	79	78	75	59	73	74	87	77	67	73
Pc	100	100	90	97	91	100	97		96	93	98	95	91	88	93	98	98	95	92	95
Dpa	100	100	91	95	89	100	98	95		90	98	96	91	85	90	97	98	91	92	95
Cha	100	100	81	87	81	100	85	84	82		86	87	95	78	89	85	91	91	79	84
Dpp	100	100	69	81	65	100	77	72	72	69		73	73	58	73	79	87	82	69	67
Cah	100	100	61	74	63	100	72	65	67	67	69		73	59	69	65	76	66	61	69
Pa	100	100	53	63	49	100	55	50	51	58	55	58		37	59	55	67	55	48	51
Dps	100	100	67	94	69	100	58	64	64	64	59	64	50		67	65	50	66	75	67
Dig	100	100	80	82	79	100	85	81	80	86	88	87	93	80		81	87	91	85	87
Eb	100	100	65	69	67	100	72	79	71	68	79	69	73	64	67		83	75	67	75
Hg	100	100	53	68	51	100	67	57	57	58	69	64	71	39	57	65		71	52	58
Sb	100	100	51	57	51	100	57	53	51	55	62	53	55	49	57	57	67		52	53
Tp	100	100	60	53	61	100	58	60	61	57	62	58	57	66	63	60	59	61		67
Cn	100	100	49	50	50	100	55	54	54	53	52	56	52	51	56	59	57	55	58	
n[1]	87	87	80	62	85	87	60	80	79	72	58	55	44	59	69	58	46	44	52	45

Species codes are the same as listed for Table 1. [1] Number of samples in which each species occur.

Table 3. Linear correlation coefficients based on nematode abundance data of the 20 most prevalent nematode species (n=87)

	Av	Dz	Dic	Pp	Ct	Lp	Dpt	Pc	Dpa	Cha	Dpp	Cah	Pa	Dps	Dig	Eb	Hg	Sb	Tp	Cn
Av																				
Dz	0.328																			
Dic	0.286	0.727																		
Pp	0.654	0.212	0.115																	
Ct	0.436	0.156	0.287	0.112																
Lp	0.204	0.818	0.751	0.128	0.230															
Dpt	0.567	0.162	0.113	0.556	0.277	0.222														
Pc	0.629	0.030	-0.070	0.661	0.333	-0.029	0.527													
Dpa	0.216	-0.196	-0.183	0.111	0.089	-0.251	0.188	0.422												
Cha	0.503	0.043	-0.076	0.731	0.143	0.054	0.527	0.829	0.253											
Dpp	0.715	0.267	0.144	0.576	0.287	0.188	0.598	0.490	0.114	0.446										
Cah	0.310	-0.198	-0.165	0.291	0.195	-0.147	0.169	0.452	0.340	0.478	0.195									
Pa	0.324	0.041	-0.042	0.286	0.147	0.026	0.432	0.408	0.102	0.391	0.535	0.087								
Dps	0.012	0.080	0.200	-0.201	0.150	0.151	-0.198	-0.245	-0.182	-0.255	-0.175	-0.003	-0.139							
Dig	0.354	-0.116	-0.059	0.137	0.273	-0.101	0.157	0.433	0.293	0.378	0.151	0.601	0.103	-0.063						
Eb	0.432	-0.070	-0.008	0.111	0.143	-0.133	0.117	0.352	0.212	0.237	0.336	0.023	0.199	-0.118	0.117					
Hg	0.571	0.066	0.054	0.594	0.242	0.080	0.344	0.549	0.260	0.490	0.606	0.654	0.203	-0.153	0.344	0.183				
Sb	0.276	-0.082	-0.041	0.102	-0.007	-0.073	0.302	0.188	0.208	0.168	0.271	0.247	0.266	-0.174	0.344	0.325	0.276			
Tp	0.052	-0.116	0.069	-0.148	0.148	-0.085	-0.196	0.117	0.161	-0.034	-0.175	0.349	-0.118	0.128	0.398	0.008	0.100	-0.079		
Cn	-0.123	-0.341	-0.059	-0.099	0.217	-0.335	-0.186	-0.043	-0.083	-0.041	-0.138	0.346	-0.029	-0.001	0.278	-0.115	0.097	0.013	0.223	

Significance levels : 5% ≥ 0.205; 1% ≥ 0.267; 0.1% ≥ 0.337
Species codes are the same as listed for Table 1.

Table 4. Chi-squared values for joint occurrences[1] based on the abundance of the 20 most prevalent nematode species (Negative values indicate a deficit of joint occurrences and consequently a negative association between species). (n=87).

	Av	Dz	Dic	Pp	Ct	Lp	Dpt	Pc	Dpa	Cha	Dpp	Cah	Pa	Dps	Dig	Eb	Hg	Sb	Tp
Av																			
Dz	*																		
Dic	*	*																	
Pp	*	*	0.74																
Ct	*	*	0.18	0.83															
Lp	*	*	*	*	*														
Dpt	*	*	0.50	7.20	*	*													
Pc	*	*	0.67	5.36	0.18	*	5.80												
Dpa	*	*	0.24	5.38	0.21	*	19.58	20.96											
Cha	*	*	0.01	4.93	0.43	*	0.68	0.68	0.14										
Dpp	*	*	1.94	18.97	1.02	*	8.70	15.23	11.63	1.45									
Cah	*	*	0.28	11.18	0.15	*	5.93	1.36	5.53	2.14	2.47								
Pa	*	*	0.06	13.12	2.00	*	1.51	0.13	0.00	10.06	1.47	3.46							
Dps	*	*	0.05	0.39	-4.31	*	-7.97	0.67	-4.18	2.95	-6.74	1.20	-12.95						
Dig	*	*	0.13	0.44	0.50	*	2.53	0.39	0.28	8.48	6.18	4.41	9.16	0.07					
Eb	*	*	1.24	0.70	0.26	*	2.17	13.75	6.88	0.36	12.52	0.40	1.47	0.42	0.04				
Hg	*	*	0.06	19.14	1.82	*	14.76	8.54	9.88	5.00	18.08	6.95	11.04	-14.20	2.62	11.16			
Sb	*	*	0.18	2.98	0.00	*	2.87	1.47	0.00	4.14	9.20	0.28	0.56	0.15	6.18	2.78	11.04		
Tp	*	*	0.02	-3.84	3.04	*	0.17	0.02	0.35	1.39	0.38	0.16	0.32	3.06	1.42	0.02	0.05	0.09	
Cn	*	*	3.52	0.26	1.87	*	0.83	1.63	2.52	0.19	0.00	1.29	0.01	0.06	2.28	3.31	0.90	0.28	1.84

* Chi-squared analysis was not appropriate due to these species occurring in 100 % of the samples.
[1] Chi-squared value for significance levels: 5% ≥ 3.80; 1% ≥ 6.60; 0.1% ≥ 10.80.
Species codes are the same as listed for Table 1.

dance and consequently species associations are likely to be due to some other factor(s).

Nematode species abundance varies according to season (Bouwman 1983, Jensen 1984). Many of the species included in this study have population minima and maxima that vary temporally (Neilson, unpublished data), potentially leading to degrees of association dependent on time of sampling.

Moens *et al.* (1999) recently reported that food densities may be less important than the relative abundances of particular food sources in determining the structure of nematode communities on tidal flats. These authors found that correlations between nematodes and dietary benthic microalgae was scale dependent.

From the sedimentary ecological factors studied, distance from a pollution source (sewage outfall) had the greatest affect on nematode species with seven significant correlations, four positive and three negative. Previously, Neilson *et al.* (1996) reported that nematode diversity, as measured by the Maturity Index (Bongers, 1990), at the study site was positively correlated ($p < 0.001$) with distance from the same pollution source. Although distance from the pollution source impacted on many nematode species, few of the tested individual heavy metals were correlated with any of the nematode species. Laboratory studies have shown that some nematode species are tolerant to heavy metal pollution (Vranken *et al.*, 1985, 1988, 1991; Sundelin & Elmgren, 1991) and field observations have provided contradictory data with Lorenzen (1974) and Tietjen (1977) noting no impact of heavy metals on nematode abundances, whereas Tietjen (1980) observed a decrease in nematode abundance. Similarly, organic C had little impact on nematode abundance, this is in accordance with previous studies by Jayasree (1976) and Lambshead (1986).

The large number of statistically positive correlations and associations between species found in this study is similar to that which Boag & Topham (1985a, b) found for a range of terrestrial nematodes. This suggests that many of the nematode species tend to be associated with each other to a lesser or greater degree. However, this contrasts with Lambshead & Hodda (1994) who reported that nematode species from a variety of biotopes, both deep-sea and estuarine, tended to be significantly discordant, *i.e.* the nematode species had a tendency to independent aggregation. There was one exception, a "mostly undisturbed" deep-sea site (Madeira Abyssal Plain) (Lambshead & Hodda, 1994). Rice & Lambshead (1994) suggested that aggregation may be increased by resource-linked disturbances, e.g. sewage-derived pollution as in this study, however, this was later discounted by Lambshead & Hodda (1994). Neilson *et al.*, (1993) from the same study site as used here assessed the aggregation of 15 of the 20 nematode species included in this study. Forty percent of the nematode species were significantly aggregated similar to that found at another polluted shallow water site (Ayr Bay) in Scotland but less than that reported from a disturbed deep-sea biotope (Lambshead & Hodda, 1994). Data from this study provide circumstantial support to Lambshead & Hodda (1994) who hypothesized that fewer species would tend to aggregate in disturbed shallow water biotopes compared with a similarly disturbed deep-sea biotopes. Boucher & Lambshead (1995) suggested that comparing non-standardized data sets should be treated with caution and that a poor sampling strategy may result in samples that do not accurately reflect the nematode community and hence distort an analysis of associations between species (Boag *et al.*, 1992).

This study has shown that the interaction within nematode communities, specifically species association, is complex and poorly understood.

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Neilson R., Boag B. Ассоциации морских нематод в приливно-отливном биотопе эстуария.

Резюме. Анализ корреляционных отношений между 20 наиболее обычными видами нематод приливно-отливного биотопа эстуария и экологических факторов осадконакопления выявил несколько существенных взаимосвязей в распространении нематод. Определена корреляционная зависимость численности семи из 20 видов нематод от расстояния до источника загрязнения, однако, только численность немногих видов нематод зависела от концентрации ионов шести различных тяжелых металлов и содержания органического углерода. Размер частиц осадков определял распространение лишь трех видов нематод, и как отдельный фактор мало влиял на их распределение. Случаи совместного обнаружения в пробах нематод 20 видов оценивали по критерию χ^2, что позволило выявить корреляции в их встречаемости. Показаны статистически достоверные случаи корреляций встречаемости нескольких видов нематод с образованием видовых ассоциаций. Эти данные находятся в противоречии с сообщениями о случаях негативных корреляций в распространении нематод в глубоководных и эстуарных биотопах.