

ECOLOGICAL CORRELATES OF ARCTIC SERPULIDAE (ANNELIDA, POLYCHAETA) DISTRIBUTIONS

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ABSTRACT

Polychaetes are traditionally considered poor biogeographic indicators because they tend to show ecological rather than geographic fidelity in their distribution. We analyzed distributions of arctic Serpulidae from ecological and biogeographic perspectives. Habitat associations were studied by principal component, correspondence, cluster, and discriminant function analyses. Records for each site included depth, temperature, salinity and sediment type, with particle size analysis and notes of whether the sample also contained rocks or shells. Temperature and depth are shown to be major environmental factors controlling distributions. Substrate associations differed significantly among studied species and appeared to be determined by sedimentation tolerances of individual species. Bathymetrically, the arctic serpulid fauna mostly consists of lower sublittoral-upper bathyal and lower sublittoral-bathyal species. Clustering by habitat produced four groups: 1) deep- and cold-water species (*Protis arctica*, *Hyalopomatus clapanetii*); 2) relatively warm-water species associated with hard sediments (*Hydroides norvegicus*, *Serpula vermicularis*, and *Pomatoceros triquetus*); 3) warm-water species associated with soft sediments (*Ditrupa*); 4) group with the highest habitat variability, associated to a larger degree with soft sediments (*Filograna implexa*, *Placostegus tridentatus*, *Protula globifera* and *Protula tubularia*). The fauna of arctic serpulids consists of North-Atlantic boreal forms with complete absence of Pacific elements. Both distribution ranges and habitat characteristics suggest that the fauna of arctic serpulids is formed by post-glacial Atlantic migrants penetrating into the Arctic with warm Atlantic currents, with the addition of deep-water relicts of the pre-glacial fauna.

INTRODUCTION

The geographic distribution of most marine animals is believed to be controlled by two major forces: geological history and current oceanographic processes (Dunton 1992). According to Ekman (1953), Fauvel (1959) and Briggs (1974) polychaete distribution patterns differ from those of other organisms, tending toward wide geographic distributions, with all major families known from all depths and oceans and many cosmopolitan species reported. Two explanations for these patterns were proposed by Fauchald (1984). First, Poly-

chaeta is an ancient group that had largely differentiated by Pangean times, and they do not show biogeographic patterns similar to those of organisms that are Mesozoic or Cenozoic in origin. Therefore, Fauchald (1984) suggested that the understanding of the distribution of recent polychaetes requires the analysis of ecological conditions rather than comparison of geographic ranges. Second, the taxonomy of polychaetes is still poorly developed, with taxonomic status of many species unresolved. The large number of reported cosmopolitan polychaete species seem to reflect the state of polychaete taxonomy rather than to indicate a tendency toward wide geographic distribution. Quite often a careful revision reveals that a "cosmopolitan" species contains a number of species with geographically restricted distributions (e.g.; Hartley 1984; Safronova 1988; Williams 1984).

As a result, studies of polychaete large-scale distribution are not very common. A few studies have been done in arctic and boreal waters (i.e. Holthe 1978; Bilyard & Carey 1980; Jirkov & Mironov 1985). On the other hand, studies of the role of abiotic and biotic factors in determining the distribution of arctic and boreal polychaetes on smaller scale are relatively numerous (e.g. Curtis 1972; Paul & Menzies 1974; Curtis & Petersen 1977; Bilyard & Carey 1979, Kondratova & Tsetlin 1979; Kristensen 1988; Bilyard 1991).

Here we analyze the distribution of members of the family Serpulidae. A recent regional revision of this group (Kupriyanova & Jirkov 1997) made it possible to alleviate the taxonomic uncertainties typical for such studies. In addition, use of one of the largest data sets on arctic polychaete habitats let us overcome the problems of small sample size and/or inadequate sampling design. Serpulids are sessile filter-feeding inhabitants mostly of hard sediments usually ignored in studies of polychaete ecology and distribution, probably because polychaete researchers traditionally concentrate their efforts on the study of in-faunal soft bottom communities.

The major objective of this study was to analyze the distribution of arctic serpulids from both historical and ecological perspectives. We quantitatively examined the distribution of these polychaetes in relation to the major abiotic factors that might account for observed geographic patterns. Also, we interpreted their geographic distribution in relation to the evolution of the Arctic Basin.

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MATERIAL AND METHODS

This study is based on extensive material collected by Russian and Soviet arctic research cruises from the turn of the century to 1986. The sampling area covered most of the Arctic Ocean, from the Faroe Islands and Iceland to the Bering Strait, from the upper shelf to abyssal depths.

Samples were taken mainly by Agassiz trawl or "Ocean" grab of 0.25 m². Because of the small number of quantitative samples taken, we could not use the information on polychaete density. For the complete taxonomic account and the detailed list of studied material, see Kupriyanova & Jirkov (1997). Only the samples containing serpulids were used for the analyses, i.e. we did not compare sites with serpulids and those without them. The following habitat parameters were available for the analyses: 1) depth (m), 2) salinity (ppt), 3) temperature (°C), and 4) sediment type. The sediment types were divided into the following categories according to the increase in particle size (coarseness): silt, silty clay, clay, silty sand, sandy silt, fine sand, coarse sand, gravel, and rocks (Kleynova 1960). If a sample, in addition to the dominant sediment, contained some fraction of another sediment, such an addition was referred to as additional sediment. The additional sediment was classified as none, small rocks, large rocks, shells, and spicules.

All analyses were performed with the Statistical Analysis System software (SAS Institute 1989). We used Waller-Duncan K-ratio Duncan Multiple Range tests on log transformed data for univariate comparisons. The log-likelihood ratio and chi-square goodness-of-fit tests were employed to test species association with sediment types (Zar 1984).

Principal component, correspondence, cluster, and discriminant function analyses (DFA) were used for multivariate analysis of data. We employed the broken-stick model (Jackson 1993) to determine the number of interpretable eigenvalues. Canonical discriminant analyses were used to distinguish characteristics of habitats used by different species. We used correlations between canonical variable(s) and original variables to interpret their importance in the model. Most of the variables were log transformed (Zar 1984) to improve the normality of data. Percentage of sediment type occurrence was used instead of ranks when DFA was performed. The assumption of equality of covariance matrices and DFA sample size requirements were considered (Morrison 1969). The determinant of the group covariance matrix ($|S|$) which is the measure of generalized variance (Morrison 1969) was used to compare variability between habitats used by different species. Mahalanobis distances (see Manly 1986) were estimated with DISCRIM procedure and used in cluster analysis. Sample sizes varied among tests because some data were missing.

For zoogeographic analysis, we grouped species by the similarity of their geographic distribution using terminology of Holthe (1978) and Bilyard & Carey (1980).

RESULTS

Distribution along depth, temperature, and salinity gradients

To account for high intercorrelation of depth, salinity, and temperature in our data set, we constructed two principal components of log transformed values of

Table 1. Descriptive statistics [mean (n, range)] of physical variables.

Species	Depth, m	T°C	Salinity, ppt
<i>Chitonopoma serrula</i>	88.0 (2, 26.0)	2.68 (1,-)	33.96 (1,-)
<i>Pomatoceros triqueter</i>	121.2 (22, 240.0)D	8.01 (21, 4.39)B	35.19 (21, 1.09)A
<i>Serpula vermicularis</i>	171.17 (30, 315.0)C	8.31 (29, 5.48)A	35.27 (28, 0.31)A
<i>Hydroides norvegicus</i>	177.7 (79, 627.0)C	7.69 (75, 12.28)B	35.13 (75, 2.08) B
<i>Filograna implexa</i>	211.8 (36, 521.0)B	7.21 (29, 9.76)B	35.10 (29, 2.08)B
<i>Protula tubularia</i>	218.1 (67, 489.0)C	3.81 (55, 11.25)D	34.95 (45, 1.43)B
<i>Ditrupea arietina</i>	235.8 (37, 445.0)B	7.58 (37, 5.23)B	35.20 (37, 1.07)A
<i>Metavermilia arctica</i>	245.0 (5, 230.0)B	4.99 (5, 4.89)G	34.28 (5, 2.26)D
<i>Placostegus tridentatus</i>	268.7 (93, 691.0)B	5.63 (86, 11.45)C	35.07 (64, 1.03)B
<i>Protula globifera</i>	349.0 (156, 3366.0)B ^b	2.01 (64, 13.02)D	34.81 (57, 4.33)C
<i>Hyalopomatus clapparedii</i>	1458.9 (19, 3480.0)A	-	-
<i>Protis arctica</i>	1498.3 (10, 1015.0)A	0.85 (10, 0.11)E	34.91(10, 0.02)B
Principal Component Loadings ^a			
PRIN1	-0.47	0.70	0.52
PRIN2	0.74	-0.001	0.67

^a-PCA of original data set; ^b- Means with the same letter are not significantly different.

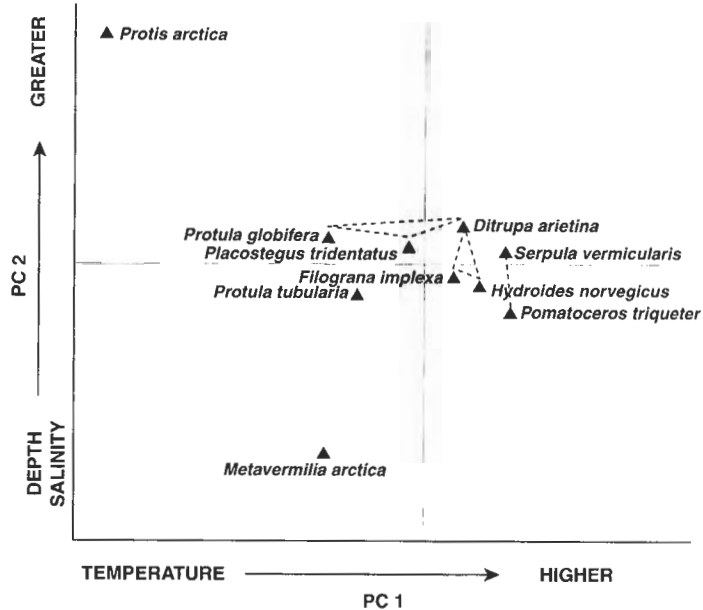


Fig. 1. The distribution of arctic Serpulidae along 2 PCA axes. Species centroids connected by lines were not significantly different (MANOVA on PC scores, $P > 0.1$).

Table 2. Distribution of arctic Serpulidae among main sediment types.

Species	Percent of samples containing:								
	silt	silty clay	clay	silty sand	sandy silt	fine sand	coarse sand	gravel	rocks
<i>Ditrupa arietina</i>	22.2	7.4	3.7	11.1	14.8	0.0	22.2	7.4	11.1
<i>Filograna implexa</i>	0.0	0.0	0.0	43.8	18.7	0.0	25.0	12.5	0.0
<i>Hyalopomatus claparedii</i>	90.9	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0
<i>Hydroides norvegicus</i>	8.5	0.0	2.1	27.7	6.4	4.3	19.2	17.0	14.9
<i>Metavermilia arctica</i>	0.0	0.0	0.0	33.3	33.3	0.0	0.0	0.0	33.3
<i>Placostegus tridentatus</i>	11.1	6.9	8.3	25.0	12.5	0.0	18.1	6.9	11.1
<i>Pomatoceros triqueter</i>	0.0	0.0	0.0	7.7	0.0	0.0	23.1	23.1	46.2
<i>Protis arctica</i>	14.3	42.9	0.0	0.0	0.0	0.0	0.0	28.6	14.3
<i>Protula globifera</i>	10.3	10.3	3.4	10.6	37.9	0.0	0.4	10.3	13.8
<i>Protula tubularia</i>	15.4	15.3	7.7	15.4	10.3	0.0	7.7	12.8	15.4
<i>Serpula vermicularis</i>	5.6	0.0	0.0	16.7	11.1	5.6	16.7	11.1	33.3

these variables and plotted the "centers" of species distributions in PC space. The first principal component axis largely ordered species along the temperature gradient (Tab. 1, Fig. 1). The second axis arranged species according to their occurrence along depth and salinity gradients. We tested for differences among PC scores because an analysis of confidence-ellipse overlap relies heavily on sample sizes, which differed among taxa in the studied group. *Chitinopoma serrula*, *Hyalopomatus claparedii* and *Metavermilia arctica* were not considered for this analysis because of their insufficient sample sizes. Distributions of *Protula globifera*, *Ditrupa arietina*, and *Placostegus tridentatus* in PC space did not differ (MANOVA on PC scores, $P > 0.1$). There were also no differences among *Filograna implexa*, *Hydroides norvegicus* and *Ditrupa arietina*, nor between *Serpula vermicularis* and *Pomatoceros triqueter* (all P 's > 0.1). Distributions of the rest of the species in PC space significantly differed (all P 's < 0.05 , Table 1, Fig. 1).

Univariate and principal component analyses revealed that *Serpula*, *Pomatoceros*, and *Ditrupa* occupied warmest waters with highest salinity. *Hyalopomatus* and especially *Protis* inhabited the deepest sites. *Metavermilia arctica* occurred in sites with relatively low salinity and low temperature. Table 1 gives the results of multiple comparisons between species along each variable measured.

Distribution among sediment types

Tables 2 and 3 give species distribution among main and additional sediment types. Table 3 also provides data on presence of spicules and shells in sediment samples. Species differed in their association with main sediment types ($X^2=108.29$, $P<0.0001$), additional sediment ($X^2=15.94$, $P<0.05$), and with presence of shells ($X^2=38.33$, $P<0.0001$). There were no differences among species

Table 3. Presence of additional sediment in samples of arctic Serpulidae*.

Species	Additional sediment			shells		spicules	
	none rocks	small rocks	large rocks	present	absent	present	absent
<i>Ditrupe arietina</i>	69.4	22.2	8.3	33.3	66.7	13.9	86.10
<i>Filograna implexa</i>	57.1	28.6	14.3	33.3	66.7	3.7	96.30
<i>Hydroides norvegicus</i>	59.2	25.0	15.8	40.0	60.0	2.7	97.30
<i>Metavermilium arctica</i>	25.0	50.0	25.0	0.0	100.0	0.0	100.0
<i>Placostegus tridentatus</i>	34.9	25.3	39.8	23.2	76.8	8.5	91.50
<i>Pomatoceros triqueter</i>	45.5	18.2	36.4	72.7	27.3	0.0	100.0
<i>Protis arctica</i>	42.9	57.1	0.0	14.3	85.7	0.0	100.0
<i>Protula globifera</i>	23.5	47.1	29.4	15.6	84.4	15.6	84.40
<i>Protula tubularia</i>	21.3	31.9	46.8	13.0	87.0	6.5	93.50
<i>Serpula vermicularis</i>	50.0	23.3	26.7	46.7	53.3	0.0	100.0

Note: * In addition to main types of sediment.

in their association with spicules ($X^2=14.66, P=0.12$). We reduced the dimensions of species-sediment contingency table (Tables 2 and 3) using correspondence analysis. To illustrate species association with different sediment types we

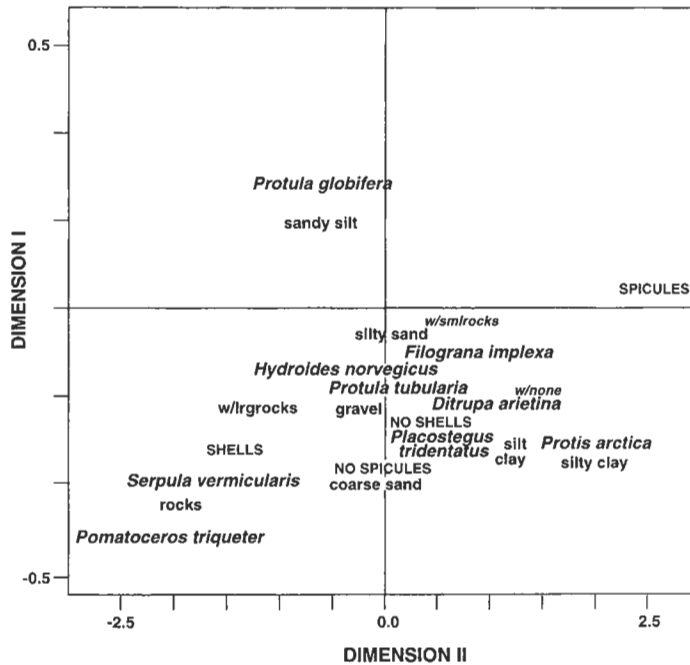


Fig. 2. The plot of "centers" of species distributions among sediment types (main, additional) and presence of shells and spicules in the canonical spaces as produced by correspondence analysis.

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<i>Hyalopomatus clapedii</i>	90.9	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0
<i>Hydroides norvegicus</i>	8.5	0.0	2.1	27.7	6.4	4.3	19.2	17.0	14.9
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Table 4. Structural correlations for discriminant function analyses of habitat variables^a measured at sites with arctic Serpulidae^b.

Variable	CAN1	CAN2	CAN3
Depth	0.91		
Temperature	-0.88		
Salinity		0.30	
Sediment coarseness	-0.40		0.61
Add. sediment coarseness		-0.79	
Presence of shells	-0.41		0.58
Explained variation (%)	75.3	13.5	6.9

^aVariables are log transformed

^bOnly correlations ≥ 0.3 are reported.

then plotted the “centers” of species distributions and sediment types in the canonical space produced by this analysis (Fig. 2). This figure shows that *Serpula vermicularis* and *Pomatoceros triqueter* are primarily associated with rocks as main sediment and large rocks as additional sediment. Both species are also associated with the presence of shells (see also Tables 2 and 3). *Ditrupea arietina*, *Protis arctica*, and, to a lesser degree, *Placostegus tridentatus* are associated with soft sediments (clay, silt, silty clay). *Ditrupea arietina* is not associated with any additional sediment. There are also weak associations between *Hydroides norvegicus* and large rocks as additional sediment, between *Protula globifera* and sandy silt, and between *Filograna implexa* and silty sand. The remaining sediment types contributed relatively little to the X^2 statistics and could not be interpreted based on Figure 2 (see Tables 2 and 3 instead). We did not analyze sediment associations of *Metavermilium arctica*, *Chitinopoma serrula*, and *Hyalopomatus clapedii* because of the small number of samples containing these species (Tables 2 and 3).

Habitat relations among species

Habitats occupied by serpulid species differed in complexity and variability (Test of Homogeneity Within Covariance Matrices, $X^2=486.39$, $df = 168$, $P<0.0001$). We did not consider presence of spicules for discriminant analyses. This variable did not differ among species habitats ($P = 0.3$) and contributed little to species separation.

Habitat occupied by *P. arctica* was the most homogeneous and had the lowest variation ($|S|=7.24 \times 10^{-14}$). Habitat used by *Pomatoceros triqueter* was significantly more variable and complex ($|S|=0.0051$). Complexity and variability of *Serpula vermicularis* and *Ditrupea arietina* habitats were also quite small ($|S|=0.042$ and 0.082 correspondingly), although significantly greater than in both previous species. Sites occupied by *Placostegus tridentatus*, *Protula globifera*, *Hydroides norvegicus*, and *Filograna implexa* were the most complex and variable ($|S|= 4.36$,

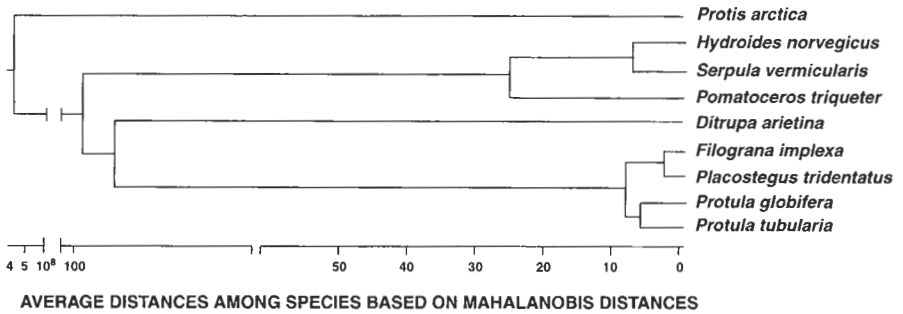


Fig. 3. Average linkage cluster analysis (UPGMA) of arctic serpulid distribution based on all environmental variables. Mahalanobis distances used to compare multivariate populations (species here) take into account correlations between variables (Manly 1986).

5.09, 5.74, and 10.00 correspondingly). Heterogeneity and variability of *Protula tubularia* habitats ($S=2.75$) were intermediate relative to those of other serpulids.

Depth and temperature contributed most to the species separation along canonical axis I (Table 4). Separation along axis II was mostly due to species association with additional sediment coarseness and, in lesser degree, with salinity. Main sediment types and shell presence ordered species along canonical axis III (Table 4).

Generally, Table 4 provides a summary of species distribution along both depth-temperature (Fig. 1; Table 1) and sediment-additional sediment gradients (Fig. 2; Tables 2 and 3). For example, *Pomatoceros* and *Serpula* occurred at relatively shallow, warm sites with large-size coarse sediment and a lot of shells. *Ditrupa* occurrence is defined by distribution of fine sediment with no rocks or shells in relatively warm waters with high salinity.

Average distance clustering of Mahalanobis distances between species resulted in separation of *Protis arctica* as the most dissimilar to the rest of the species in the family with respect to habitat used (Fig. 3). This distance should not be interpreted numerically, but rather viewed as an indicator of the large difference between *Protis arctica* and others with respect to depth gradient. *Filograna implexa* and *Placostegus* occurred in the most similar habitats. The habitat used by *Protula globifera* was most like that of *Protula tubularia*. The habitat occupied by *Hydroides norvegicus* was most similar to that of *Serpula*.

Zoogeographic grouping

Most arctic serpulids show a high degree of eurybathy (Table 5). Their bathymetric distribution falls into the following partially overlapping categories: sublittoral species (*Chitinopoma serrula* only), species inhabiting lower sublittoral and upper bathyal zone (depth range of 290-715 m, see Table 5), and bathyal

Table 5. Bathymetric and zoogeographic categories of arctic Serpulidae.

Species	Depth distribution, m		Zoogeographic grouping
	min-max,	range	
<i>Chitinopoma serrula</i>	75-101	26	Atlantic-boreoartic
<i>Ditrupa arietina</i>	115-560	445	Atlantic-boreoartic*
<i>Filograna implexa</i>	84-605	521	Atlantic-boreoartic*
<i>Hyalopomatus claparedii</i>	142-3622	3480	Arctic
<i>Hydroides norvegicus</i>	23-650	627	Atlantic-boreoartic*
<i>Metavermilina arctica</i>	120-350	230	Atlantic-boreoartic
<i>Placostegus tridentatus</i> ****	24-715	691	Atlantic-boreoartic
<i>Pomatoceros triquetus</i>	50-290	240	Atlantic-boreoartic*
<i>Protis arctica</i>	805-1820	1015	Arctic **
<i>Protula globifera</i>	18-3384	3366	Atlantic-boreoartic
<i>Protula tubularia</i>	11-500	489	Atlantic-boreoartic
<i>Serpula vermicularis</i>	110-425	315	Atlantic-boreoartic ***

1-1* Also known from the Mediterranean and subtropical North Atlantic.

** The species has been reported from the Mediterranean (Ben Eliahu & Fiege 1996) and from various locations outside the Arctic Ocean (see Kupriyanova & Jirkov 1997).

*** *Serpula vermicularis* has been erroneously considered a cosmopolitan species. True distribution range outside North Atlantic is not known.

**** Has also been reported from the Mediterranean and Indo-West Pacific.

species with upper limit of the depth range exceeding 1000 m (*Protis arctica*, *Hyalopomatus claparedii*, and *Protula globifera*). No abyssal species were found. The first two bathymetric categories consist of boreal Atlantic-boreoartic species (found in the arctic basin and in the boreal waters of the Atlantic). The last group includes two arctic species (found north of 66.5° N): *Protis arctica* and *Hyalopomatus claparedii*, as well as an extremely eurybiotic Atlantic-boreoartic *Protula globifera*, having the widest geographic distribution within the Arctic Ocean. No boreal-Pacific (occurring in the Bering Sea and the Sea of Okhotsk) or Pacific-boreoartic species (occurring in the Arctic Basin and the boreal waters of the Pacific) were found.

DISCUSSION

The modern biogeography of the Arctic Ocean is a result of the effects of Quaternary glaciation almost eradicating the shelf benthic assemblages. These events are superimposed on a very broad arctic shelf, which results in a complex of estuarine seas (Dayton et al. 1994). Arctic benthic communities are characterized by a relatively young fauna with most species having colonized the region since the last ice age (Zenkewitch 1963; Knox & Lowry 1977; Bilyard & Carey 1980; Golikov & Scarlato 1989). As a result, arctic fauna comprises species of Atlantic and/or Pacific affinity with very few endemics (Briggs 1974; Gol-

ikov & Scarlato 1989). The distribution patterns of arctic serpulids reflect these characteristics of the Arctic Basin and also show some specific features.

First, species richness is extremely low in comparison with that of temperate and tropical regions. The decrease in species richness toward the polar regions is well documented for four major groups of shelf benthos (crustaceans, echinoderms, mollusks, and polychaetes) and low diversity is typical for entire fauna of the Arctic Basin (Dunbar 1982). However, species richness is also very low in Serpulidae even when compared with that of other families of arctic polychaetes (e. g. Holthe 1978; 1992).

Second, both distribution ranges and ecological characteristics of arctic species show that almost the entire recent serpulid fauna consists of species of Atlantic affinity with complete absence of boreal Pacific elements. Generally, the Pacific element is poorly represented in the present arctic fauna (Dayton 1990). Bilyard & Carey (1979) reported the absence of bathyal Pacific boreoarctic polychaetes and attributed it to the effect of the shallow Bering Strait serving as a bathymetric barrier to dispersion. No serpulids were found in the northern part of the Bering Sea (Uschakov 1955; Kupriyanova & Rzhavsky 1993). Only *Protis arctica*, *Hyalopomatus clapedii* and *P. globifera* are known east of Lomonosov Ridge, whereas the rest of the species are found mainly in the Norwegian and Barents Seas.

The observed pattern of predominant serpulid distribution in the Norwegian and Barents Seas is explained by the fact that the Atlantic Boreal Water Mass extends to this area from the surface to 600 m. The arctic shelves that are influenced by warm Atlantic waters are among the most productive marine areas because of the convergences of different current systems (Grebmeier & Barry 1991). In the Barents Sea, which has the most diverse fauna in the Arctic, the high productivity results from the mixing of the cold arctic and warm Atlantic water masses. Unlike any other arctic water mass, the Barents Sea also has limited riverine input resulting in a limited influx of sediment (Dayton et al. 1994).

Third, all species with the exception of sublittoral *Chitinopoma serrula*, are eurybathic and can be found within bathymetric ranges varying from 240 to 3480 m. The eurybathic nature of western arctic species has been stressed by Nesis (1984). He proposed that the predominantly eurybathic distributions in the western arctic and stenobathic distribution in the eastern Arctic is the result of the differences in the nature of Quaternary glaciation in the two regions. According to the evidence presented in his paper, the juxtaposition lines of glaciers in the region of Norwegian and Barents Seas lay at depths of 500-600 m and made it impossible for stenobathic shallow-water species to survive the glaciation.

According to our results, depth and temperature gradients appear to exert primary control over the distribution patterns of arctic Serpulidae (Table 4). Similar results were found for other arctic polychaetes. Bilyard & Carey (1979)

identified depth-related processes as controlling polychaete distribution in the Canadian Arctic. Polychaete densities also demonstrated a marked relation to depth in a number of species commonly occurring in the Arctic (Curtis 1972). However, for arctic serpulids the observed effect of depth and temperature on the distribution can be explained by the prevailing current system. Not accidentally, 9 of 12 species of arctic serpulids confined to the western Arctic also have bathymetric ranges not exceeding 700 m, the depth of penetration of the warm Atlantic current. The evidence indicates that arctic serpulid fauna predominantly consists of post-glacial Atlantic immigrants. The only arctic endemic, *Hyalopomatus claparedii*, is able to inhabit much greater depths, and tolerate low arctic temperatures. This species is likely to be a relict of the pre-glacial era, that found shelter in the low bathyal zone during Pliocene-Pleistocene variations in sea level.

Finally, sediment types inhabited by arctic serpulids within the species ranges are quite diverse and vary among species. It appears that when other ecological conditions are favorable, serpulids can inhabit clay, muddy or silty bottom provided that the soft sediments contained some solid substances (stones, shells) for tube attachment. As expected, the only species not associated with any kind of hard substrate is *Ditrupa arietina*, a free-living serpulid species preadapted to inhabiting soft sediments.

The danger of being buried in soft sediments can pose a problem for sessile filter-feeders and may potentially be an important factor limiting their geographic distribution. Serpulids seem to be able to deal with high sedimentation by changing the shape and direction of tubes (e. g. Hartman-Schröder 1971, ten Hove & van der Hurk 1993, and personal observation). If so, standing erect tubes should be observed in waters with low current and high sedimentation rate, while tubes completely attached to the sediment should indicate water movements (currents, tides) with low sedimentation. The general tube morphology of the considered species supports this observation. *Protis arctica*, *Placostegus tridentatus*, *Protula globifera*, and *Filograna implexa* commonly associated with soft substrata have erect upward directed tubes as a rule, whereas *Serpula*, *Hydroides* and *Pomatoceros* have mostly attached tubes. This relationship of tube morphology to sedimentation needs to be studied further.

For serpulids the sediment composition is obviously an important determinant of local small-scale distribution and habitat selection within the inhabited geographical range (see also Bilyard & Carey 1979). However, it also can be a factor affecting their large-scale geographic distribution. The near absence of serpulids in the wide shallow shelves of Siberian Seas may be partly explained by large inputs of sediments from rivers flowing into the Arctic Basin. This river influx results in low salinity shelf water and sediments dominated by mud and clay.

Thus, the effect of Quaternary glaciation, warm Atlantic currents, high productivity and low riverine input in the western Arctic (especially in the Norwe-

gian and Barents Seas), and low temperatures and high sedimentation rates due to high riverine input in the shelf of eastern Arctic seem to be the factors shaping the pattern of serpulid distribution in the Arctic Basin. The geographic distribution of arctic serpulids appears to be a complex interplay of historical and ecological factors. The better understanding of the relative importance of these factors in the distribution of polychaetes requires more studies combining ecological and zoogeographic approaches with taxonomic revisions of studied groups.

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