Pechora Sea Environments: Past, Present, and Future

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THE ZOOBENTHOS OF THE PECHORA SEA REVISITED: A COMPARATIVE STUDY

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Abstract

Samples of benthic macrofauna from the Pechora Sea (southeastern part of the Barents Sea) were collected during r/v “Dal’nie Zelentsy” cruise in 1992. Parallel sampling and analyses by Russian and Norwegian scientists allow comparing the two datasets, and thus integrating Russian and other international knowledge on benthic fauna of this region. Contrary to the previous opinion about low biodiversity in this region, the fauna richness (446 taxa) appeared to be two times larger. Independent of differences in the sampling equipment and washing procedure, the number of taxa in both Russian and Norwegian datasets was comparable. Some discrepancies in the records of certain faunal groups are attributed to differences in species distribution and identification literature on some systematic groups. In the Russian data, the abundance varied from 666 to 2378 ind./m², and the biomass - from 8 to 920 g/m². Community-based approach to the numerical analyses of benthic production compared with faunal assemblages (Dahle et al., 1998) shows a general similarity in species composition and abundance distribution only in environmentally stressed areas, where the benthic organisms generally have lower biomass. In the largest part of the Pechora Sea, there is greater heterogeneity among dominant species within the Dahle et al. (1998) data, because the present work incorporates production derived from abundance and biomass.

Introduction

Analyses of benthic communities could be used to assess the effects of different human impacts (Pearson and Rosenberg, 1978), as well as to perform retrospective studies of climatic changes (Deryugin, 1924). Russian scientists have carried out investigations of benthic fauna in the arctic seas (Deryugin, 1928; Pergament, 1945; Zenkevich, 1963). Denisenko et al. (1995) reviewed the studies of macrobenthic fauna of the Pechora Sea (southeastern part of the Barents Sea). However, the focus of these investigations has varied to such an extent that it is difficult to compare the results of the studies over time. In addition to the problem of compensating for and standardizing the different approaches used throughout the years, another important issue is the differences in methodology and analytical approaches used between Russian and other, international laboratories. In Soviet times, a large amount of Russian data did not reach the international scientific community. Therefore, there is an urgent need for mutual exchange of methods and results, as well as for building bridges to earlier findings.
The Murmansk Marine Biological Institute of the Russian Academy of Sciences and Akvaplan-niva, Norway, have been cooperating in the studies of the arctic benthic macrofauna since 1990. In 1992, a cruise aboard RV "Dal'nie Zelentsy" was organized to study the benthic fauna of the Pechora Sea. During this cruise, parallel sets of samples were collected, using the standard methodology of the respective Russian and Norwegian participating institutes. The Norwegian team used a 50 kg 0.1m² Van Veen grab (Van Veen, 1933), and the samples were washed through a 1-mm-meshsize sieve with round holes. The description of the faunal associations was based on a numerical quantification of the species present, as well as on the ecology of the dominant taxa. Using canonical correspondence analyses (CCA), the connection between the faunal data and environmental variables was analyzed (Dahle et al., 1998).

The present work documents the findings of the Russian team, who used a modified Petersen grab (Petersen and Boysen Jensen, 1911) with a sampling area of 0.25 m². An integrated, community-based approach to the numerical analyses was applied, combining the species biomass and abundance into a purpose-devised formula to achieve an index of benthic production. The latter is a suitable parameter for estimating the role of each species in a community because it is based on a combination of both abundance and biomass. Although the two datasets are not extensive enough to be used to reveal statistically significant relations between the two approaches, the fact that both sets of samples were collected at the same locations and at the same time allows for a first comparison of the results from the two different sampling and analytical approaches.

Study area

The Pechora Sea occupies the southeastern part of the Barents Sea and is bordered by Kolguev, Novaya Zemlya, and Vaigach islands in the west, north, and east, respectively, and by the mainland in the south (Fig. 1).

The Pechora Sea is a heterogeneous area in terms of water depth (Fig. 1) and sediment type (Adrov and Denisenko, 1996; Dahle et al., 1998). Temperature and salinity of bottom and surface water layers show strong seasonal and spatial variations. Bottom water temperatures reach their maximum in August-September, and generally range from -1°C in the north to 6°C in the southwest, close to the coast (Adrov and Denisenko, 1996). The average bottom salinity in the open part of the Pechora Sea ranges from 34 in winter to 30-31 in early spring due to large amounts of freshwater runoff from the Pechora River and ice melting.

In short, the Pechora Sea forms a mixing zone of four main water masses (Il'in and Matishov, 1992): coastal water masses in the south, waters of Atlantic origin in the central parts, Barents Sea bottom water in the deep trench south of Novaya Zemlya, and Arctic water extending from the Kara Strait and flowing northwards along the Novaya Zemlya coast.

Material and methods

Sampling
Sampling was carried out in July 1992 from the MMBI research vessel "Dal'nie Zelentsy". The station locations (Fig. 1) correspond to those of Dahle et al. (1998). Two additional stations, 6a and 7a, were sampled in the western open sea.

Quantitative samples were collected using an Ocean grab (Lisitzin and Udintsev, 1955) with a sampling area of 0.25 m². The weight of this grab is c. 70-90 kg depending on the additional weight, and its penetration into the ground is 20-25 cm depending on sediment softness. Two or three replicate samples were collected at each sampling station. The samples were gently flushed through a nylon net bag with a square meshsize of 0.75 mm (i.e. diagonal opening close to 1 mm). After washing to remove fine sediment particles, the remaining sediment and animals were fixed in 4% formaldehyde buffered by sodiumtetraborate (hexamine).

**Laboratory analyses**

In the laboratory, the samples were sieved through a soft nylon mesh with a square meshsize of 0.5 mm in running water to remove formaldehyde and any remaining fine sediment particles. The animals were sorted to different taxonomic groups using a microscope. They were preserved in 70% ethanol, and, subsequently, identified either to species or the lowest taxonomic level possible. Specimens that could not be accurately identified to species level due
to taxonomic difficulties (Spongia, Cnidaria, Nematoda, Sipuncula, Tunicata) were identified to generic or family levels, and recorded in the total number of 'taxa'.

The identified species in each sample were counted and weighed (wet mass in alcohol) to 3 decimal points using a calibrated scale. Molluscs, bryozoans, and barnacles were weighed including shell skeleton. The annelids were removed from their tubes for weighing, except the polychaete Spiochaetopterus typicus, which was weighed inclusive of tube, mainly because it is entirely self-secreted by the animal, and, also, because it is difficult to remove the tube without destroying the fragile animal.

**Numerical analyses**

The species numbers and abundance data from the two or three 0.25 m² replicates were combined for each station, giving a total sampling area for each station of 0.5 m² or 0.75 m², respectively. For all stations a mean value for the number of taxa per 0.25 m² was calculated, while the abundance and biomass were calculated per one square meter.

Clustering of the benthic communities was carried out using similarities of samples based upon calculations of species production. Estimation of a given species production from its abundance and biomass was suggested by Brey (1990) and Denisenko and Denisenko (1990). In our calculations, the formula derived by Denisenko and Denisenko (1990) was used to figure out the production of the identified species:

\[ P = k B_s^{0.75} N_s^{0.25} \]

where \( P \) is the approximate production of a species in a given sample per year or seasonal growth (in the same units as biomass), \( B_s \) biomass, and \( N_s \) abundance of 's'-species.

To calculate the inter-station similarity, we applied the Czekanowski-Soerensen index (Czekanowski, 1909; Soerensen, 1948). The production value of each species was used in the calculations as follows:

\[ C = 2 \cdot \frac{\text{min}(P_{sa}, P_{sb})}{(P_{sa} + P_{sb})} \]

where \( P_{sa} \) is the estimated production of 's'-th species at station 'a', \( P_{sb} \) the estimated production of 's'-th species at station 'b'.

To determine faunal communities, a standard hierarchical clustering procedure (Pesenko, 1982) with the average linkage method was used. To define the level at which the samples should be assigned to separate communities, the average level of similarity for the whole matrix was calculated (Sirotinskaya, 1975).

The dominant species, after which the communities are named, are the species having the highest "validity". The validity of a given species is calculated as the product of the species production and its frequency of occurrence within samples incorporated into the community.

Station grouping by their similarity on the basis of standardized environmental characteristics (such as depth, bottom temperature, salinity, dissolved oxygen content, type of bottom sediments) was carried out by hierarchic clustering using Euclidean distances as similarity coefficients.
Results

Species composition

A total of 446 different taxa were recorded, of which 343 were identified to species level. The number of taxa at different stations varied between 15 and 129 (per 0.25 m²).

A total of 16 phyla, 19 classes, and 134 families were recorded. The species number of different systematic groups is presented in Table 1 and Fig. 2A. The highest species richness (129 taxa per 0.25 m²) was recorded on the mixed bottom sediments near the Kata Gate Strait (St.19, 21, see Fig. 2A).

Table 1. Fauna structure in the Pechora Sea, comparison of the two studies carried out during the same cruise in 1992.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Russian data set</th>
<th>Norwegian data set (after Dahle et al., 1998)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total taxa</td>
<td>Species</td>
</tr>
<tr>
<td>Protozoa</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Porifera</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>31</td>
<td>23</td>
</tr>
<tr>
<td>Nemertini</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Nematoda</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Sipuncula</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Priapulida</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Echiurida</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>118</td>
<td>90</td>
</tr>
<tr>
<td>Pantopoda</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Crustacea</td>
<td>102</td>
<td>76</td>
</tr>
<tr>
<td>Mollusca</td>
<td>93</td>
<td>72</td>
</tr>
<tr>
<td>Bryozoa+</td>
<td>61</td>
<td>56</td>
</tr>
</tbody>
</table>

Brachiopoda

| Echinodermata    | 22               | 17      | 17         | 14      |
| Tunicata         | 4                | 1       | 6          | 4       |

Total | 446 | 416
The faunal structure of zoobenthos at different stations in the Pechora Sea is illustrated in Fig. 2. A - According to the data set collected by the Russian team in 1992; B - according to the data set collected by the Norwegian team in 1992.

Key: ANN - Annelids; CR - Crustaceans; ED - Echinoderms; MO - Molluscs; OTH - others. Diameter of a circle reflects the number of species found at each station.

The remaining stations located on sandy-mud or muddy-clay sediments contained from 71 to 85 taxa. An impoverished benthic fauna was found in and close to the Pechora Bay (15 and 41 taxa at St. 29 and St. 27, respectively). At all stations Polychaeta showed the highest taxonomic diversity.

Abundance

The highest number of individuals at stations 3, 7a, 13 and 24 (Fig. 3A) exceeded 2000 ind./m². The lowest abundance was recorded at St. 27 (666 ind./m²). In general, polychaetes represented the most abundant faunal group, and their abundance varied from 152 (St. 21) to 2248 ind./m² (St.13). Polychaetes predominated throughout the whole area except the Pechora Bay (St. 29) and Kara Strait area (St. 19, 21), where crustaceans were dominant with the abundance equal to 1066, 489 and 465 ind./m², respectively. The highest abundance of molluscs (573 ind./m²) was registered at St. 6, and the lowest at stations 12 and 27 (38 and 44 ind./m², respectively). Echinoderms were not numerous, and their frequency varied from 6 (St. 6a, 7) to 188 ind./m² (St. 6).
Biomass

Fig. 4 presents variations in biomass within the study area. The biomass ranges between 108 and 446 g/m² in the northern part of the Pechora Sea with mixed bottom grounds. At St. 6, to the northeast of Kolguev Island, the recorded biomass equals 710 g/m². However, this high value is attributed to the presence of a single large specimen of the echinoderm Henricia scorikovi. Exclusion of this species reduces the biomass value down to approximately 400 g/m². Stations 8, 21, and 24 (the latter two on coarse sediments) are characterized by intermediate biomass values (108, 103, and 122 g/m², respectively). In the Pechora Bay, the biomass is 44 g/m². The lowest biomass, 8 g/m², is found at St. 27, on sandy sediments in the southern part of the study area.

Community structure

Based on the similarity analyses, the benthic fauna of the 16 stations may be grouped into six communities, subsequently referred to as Groups A to F (Fig. 5). Fig. 6 shows the spatial distribution of these communities, and their main characteristics are given in Table 2. The community referred to as Group A includes only one station (7a) located southwest of Novaya Zemlya at the depth of 120 m on soft silty clay sediments with a small sand portion. This community is dominated by two species, Ctenodiscus crispatus and Macoma calcarea.

Group B (Table 2) is made up of 5 stations (3, 8, 11, 12, 13, 14), four of which (8, 12, 13, 14) are located close to each other in the depression south of Novaya Zemlya, at the depths between 180 and 250 m, which is the deepest part of the Pechora Sea. Stations 3 and 11 are located in shallow areas - in the strait between Kolguev Island and the mainland, and in the Chernaya Fjord. At all five stations characterized by high concentration of organic matter in the sediment surface and subsurface, deposit feeders predominate. The dominant species is Spiochaetopterus typicus.

Group C (Table 2) is made up of stations 6, 6a, 7, 19, and 20, all at depths between 88 and 126 m on sandy mud sediments. Stations 6, 6a, and 7 are influenced by currents from the western Barents Sea, while stations 19 and 20 are influenced by the Kara Sea water. This community is dominated by the mobile filter-feeder Tridonta borealis. This species has neither the highest abundance nor the biomass, but it occurs in more than half of the samples, which in combination gives the highest species validity within the community. Despite the large biomass of Henricia scorikovi, its very low frequency and abundance prevent it from being a dominant or subdominant species for this community.

Group D (Table 2) comprises station 21 located in the Kara Strait. This station is influenced by strong bottom currents and is, therefore, characterized by mixed sediments with a large portion of coarse components such as gravel and pebbles. Due to its high biomass, the dominant species Strongylocentrotus pallidus has a twice greater validity than the subdominant species, the erect filter-feeding bryozoan Myriapora gracilis, even though the latter is very abundant and present in all samples.
Fig. 3. Abundance (ind./m²) of the bottom fauna and the share of different systematic groups. A – According to the data set collected by the Russian team in 1992; B – according to the data set collected by the Norwegian team in 1992. Key for group description is the same as in Fig. 2.

Fig. 4. Biomass (g/m²) of the bottom fauna and the share of different groups in the study area. Key for group description is the same as in Fig. 2.
Fig. 5. Cluster diagram showing station grouping based on the similarity of the fauna production data. A – Ctenodiscus crispatus-Macoma calcarea community; B – Spiochaetopterus typicus community; C – Tridonta borealis community; D – Strongylocentrotus pallidus community; E – Serripes groenlandicus community; F – Macoma balthica community.

Fig. 6. Distribution of bottom communities in the study area. Key is the same as in Fig. 5.
Table 2. The ten most significant taxa according to their validity *) for every of the six established benthic communities (A-F) in the study area of the Pechora Sea. Average abundance, biomass, frequency, and relative production are indicated for each taxon. Additionally, average biomass, number of species, and samples for every community are given.

<table>
<thead>
<tr>
<th>Community group</th>
<th>Abundance, with ten most common taxa</th>
<th>Biomass, g/m²</th>
<th>Frequency of occurrence</th>
<th>Relative production</th>
<th>Species validity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group A</strong></td>
<td>Ctenodiscus crispatus</td>
<td>34</td>
<td>68.11</td>
<td>0.80</td>
<td>57.06</td>
</tr>
<tr>
<td></td>
<td>Macoma calcarea</td>
<td>529</td>
<td>35.87</td>
<td>0.40</td>
<td>70.10</td>
</tr>
<tr>
<td></td>
<td>Yoldia amygdalae</td>
<td>46</td>
<td>18.12</td>
<td>0.60</td>
<td>22.67</td>
</tr>
<tr>
<td></td>
<td>Ophiocten sericeum</td>
<td>44</td>
<td>8.52</td>
<td>1.00</td>
<td>12.84</td>
</tr>
<tr>
<td></td>
<td>Macoma moesta</td>
<td>660</td>
<td>28.88</td>
<td>0.20</td>
<td>63.14</td>
</tr>
<tr>
<td></td>
<td>Portlandia arctica</td>
<td>33</td>
<td>16.73</td>
<td>0.60</td>
<td>19.15</td>
</tr>
<tr>
<td></td>
<td>Nuculana pernula</td>
<td>40</td>
<td>9.67</td>
<td>0.60</td>
<td>13.71</td>
</tr>
<tr>
<td></td>
<td>Lumbriconereis sp.</td>
<td>340</td>
<td>1.68</td>
<td>1.00</td>
<td>5.75</td>
</tr>
<tr>
<td></td>
<td>Scalibregma inflatum</td>
<td>269</td>
<td>1.19</td>
<td>1.00</td>
<td>4.53</td>
</tr>
<tr>
<td></td>
<td>Goflinea margaritacea</td>
<td>4</td>
<td>35.76</td>
<td>0.20</td>
<td>20.68</td>
</tr>
<tr>
<td><strong>Number of samples:</strong> 5</td>
<td><strong>Number of taxa:</strong> 11</td>
<td><strong>Average biomass:</strong> 145.38</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| **Group B**     | Spiochaetopterus typicus         | 220           | 110.86                 | 0.82                | 129.91           | 107.32           |
|                 | Maldane sarsi                    | 284           | 22.27                  | 1.00                | 38.85            | 38.85            |
|                 | Chaetozoane setosa               | 516           | 2.42                   | 0.95                | 9.12             | 8.72             |
|                 | Ctenodiscus crispatus            | 11            | 21.65                  | 0.47                | 16.50            | 7.89             |
|                 | Yoldia amygdalae                 | 74            | 21.49                  | 0.21                | 23.47            | 5.10             |
|                 | Priapulus caudatus               | 17            | 6.95                   | 0.56                | 5.15             | 3.48             |
|                 | Lumbriconereis sp.               | 288           | 1.22                   | 0.69                | 4.74             | 3.30             |
|                 | Ophiocten sericeum               | 35            | 3.87                   | 0.47                | 6.70             | 3.20             |
|                 | Nicania montagui                 | 37            | 7.78                   | 0.26                | 11.26            | 2.93             |
|                 | Thyasira gould                   | 135           | 1.58                   | 0.52                | 4.63             | 2.41             |
| **Number of samples:** 23 | **Number of taxa:** 257 | **Average biomass:** 166.80 |

| **Group C**     | Tridonta borealis                | 39            | 126.34                 | 0.55                | 87.54            | 48.63            |
|                 | Travisia forbesii                | 27            | 155.36                 | 0.33                | 99.65            | 33.21            |
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Henricia skorikovi 10  698.00  0.11  241.48  26.83
Cillatocardium ciliatum 9  80.01  0.55  45.33  25.18
Golfinia margaritacea 17  99.08  0.33  63.75  21.25
Nicania montagui 62  16.55  0.88  21.48  19.09
Balanus crenatus 94  82.54  0.22  81.78  18.17
Spiochaetopterus typicus 64  9.18  0.88  14.31  12.72
Maldane sarsi 97  5.39  0.88  10.66  9.48
Macoma calcarea 28  51.58  0.22  41.2  59.16

Number of samples: 9, Number of taxa: 229, Average biomass: 427.25

Group D

<table>
<thead>
<tr>
<th>Species</th>
<th>Count</th>
<th>Weight</th>
<th>Biomass</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strongylocentrotus pallidus</td>
<td>57.72</td>
<td>12</td>
<td>98.36</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Myriapora subgracilis</td>
<td>212</td>
<td>11.72</td>
<td>1.00</td>
<td>23.91</td>
<td>23.91</td>
</tr>
<tr>
<td>Celleporina incrassata</td>
<td>36</td>
<td>11.10</td>
<td>1.00</td>
<td>14.86</td>
<td>14.86</td>
</tr>
<tr>
<td>Macoma calcarea</td>
<td>60</td>
<td>17.36</td>
<td>0.50</td>
<td>23.67</td>
<td>11.83</td>
</tr>
<tr>
<td>Ophiura robusta</td>
<td>88</td>
<td>6.24</td>
<td>0.50</td>
<td>12.09</td>
<td>6.04</td>
</tr>
<tr>
<td>Alvania vindula</td>
<td>8</td>
<td>6.80</td>
<td>0.50</td>
<td>7.08</td>
<td>3.54</td>
</tr>
<tr>
<td>Nephtys ciliata</td>
<td>4</td>
<td>7.28</td>
<td>0.50</td>
<td>6.27</td>
<td>3.13</td>
</tr>
<tr>
<td>Rhodine gracilior</td>
<td>86</td>
<td>0.40</td>
<td>1.00</td>
<td>1.52</td>
<td>1.52</td>
</tr>
<tr>
<td>Polychaeta varia</td>
<td>4</td>
<td>1.27</td>
<td>1.00</td>
<td>1.48</td>
<td>1.40</td>
</tr>
</tbody>
</table>

Number of samples: 2, Number of taxa: 112, Average biomass: 150.91.

Group E

<table>
<thead>
<tr>
<th>Species</th>
<th>Count</th>
<th>Weight</th>
<th>Biomass</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serripes groenlandicus</td>
<td>10</td>
<td>55.89</td>
<td>0.66</td>
<td>35.01</td>
<td>23.34</td>
</tr>
<tr>
<td>Stegophiura nodosa</td>
<td>135</td>
<td>4.88</td>
<td>0.77</td>
<td>11.04</td>
<td>8.58</td>
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<tr>
<td>Bivalvia g.sp.</td>
<td>61</td>
<td>5.28</td>
<td>0.77</td>
<td>9.17</td>
<td>7.13</td>
</tr>
<tr>
<td>Ascidiacea g.sp.</td>
<td>34</td>
<td>5.37</td>
<td>0.44</td>
<td>8.49</td>
<td>3.77</td>
</tr>
<tr>
<td>Pelonaia corrugata</td>
<td>55</td>
<td>11.16</td>
<td>0.22</td>
<td>16.50</td>
<td>3.66</td>
</tr>
<tr>
<td>Owenia fusiformis</td>
<td>74</td>
<td>1.23</td>
<td>1.00</td>
<td>2.78</td>
<td>2.78</td>
</tr>
<tr>
<td>Modiolus modiolus</td>
<td>12</td>
<td>23.72</td>
<td>0.11</td>
<td>20.00</td>
<td>2.22</td>
</tr>
<tr>
<td>Myrochele oculata</td>
<td>338</td>
<td>0.35</td>
<td>1.00</td>
<td>1.93</td>
<td>1.93</td>
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<tr>
<td>Scoloplos armiger</td>
<td>68</td>
<td>0.55</td>
<td>1.00</td>
<td>1.78</td>
<td>1.78</td>
</tr>
<tr>
<td>Edwardsiidae g.sp.</td>
<td>23</td>
<td>1.14</td>
<td>0.77</td>
<td>2.25</td>
<td>1.75</td>
</tr>
</tbody>
</table>

Number of samples: 9, Number of taxa: 146, Average biomass: 70.64

Group F

<table>
<thead>
<tr>
<th>Species</th>
<th>Count</th>
<th>Weight</th>
<th>Biomass</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macoma balthica</td>
<td>245</td>
<td>38.51</td>
<td>1.00</td>
<td>60.39</td>
<td>60.39</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Biomass of Individuals</th>
<th>Biomass</th>
<th>Biomass</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pontoporeia femorata</td>
<td>790</td>
<td>2.36</td>
<td>1.00</td>
<td>10.07</td>
<td>10.07</td>
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<tr>
<td>Halicrnostus spinulosus</td>
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<td>1.00</td>
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<td>3.75</td>
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<tr>
<td>Spionidae g.sp.</td>
<td>71</td>
<td>0.78</td>
<td>1.00</td>
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<tr>
<td>Diastylis sulcata</td>
<td>201</td>
<td>0.22</td>
<td>1.00</td>
<td>1.22</td>
<td>1.22</td>
</tr>
<tr>
<td>Nemertini g.sp.</td>
<td>16</td>
<td>0.66</td>
<td>1.00</td>
<td>1.40</td>
<td>1.75</td>
</tr>
<tr>
<td>Nephtys minuta</td>
<td>208</td>
<td>0.07</td>
<td>1.00</td>
<td>0.56</td>
<td>0.56</td>
</tr>
<tr>
<td>Polychaeta varia</td>
<td>12</td>
<td>0.12</td>
<td>1.00</td>
<td>0.36</td>
<td>0.36</td>
</tr>
<tr>
<td>Amphipoda g. sp.</td>
<td>72</td>
<td>0.04</td>
<td>1.00</td>
<td>0.29</td>
<td>0.29</td>
</tr>
<tr>
<td>Yoldiella intermedia</td>
<td>10</td>
<td>0.50</td>
<td>0.16</td>
<td>1.05</td>
<td>0.17</td>
</tr>
</tbody>
</table>

Number of samples: 6, Number of taxa: 16, Average biomass: 44.08

*) Species validity is the species production multiplied by their frequency of occurrence.

Group E (Table 2) encompasses stations 24, 26, and 27 located in the shallow southern part of the study area on sandy sediments with low organic content. The area is influenced by coastal water masses with highly variable temperature and salinity. The benthic community is dominated by filter-feeding bivalve Serriptes groenlandicus. Due to its large biomass, S. groenlandicus has a validity three times higher than that of the subdominant species, the carnivorous brittle-star Stegophia nodosa, although the abundance of the latter species is ten times higher than that of the former.

Group F (Table 2) contains samples from St. 29 in the estuarine part of the Pechora Bay. The muddy sediments in this area are under strong influence of brackish water. Species richness, abundance, and biomass are relatively low; the dominant species is the deposit feeding mollusc Macoma balthica. Although the abundance of the subdominant species, the amphipod Pontoporeia femorata, is approximately three times higher than that of M. balthica, the latter taxon has a far higher biomass (38.5 g/m²).

Discussion

Zenkevich (1927) recorded only 220 species of macrozoobenthos from the Pechora Sea, and considered the region to be relatively poor in species. The number of species recorded during the present study is 446, while the Norwegian team reported 416 species (Dahle et al., 1998). Some discrepancies were found between the two datasets in certain faunal groups, for instance, the phyla Polychaeta and Crustacea, resulting from differences in species identifications and synonyms of the taxa in the taxonomic literature used by the two teams. In addition, the phylum Hydroidea, was identified to species level in the Russian but not the Norwegian samples.

Nevertheless, the two datasets demonstrate similar results in terms of species composition and spatial distribution of species numbers (Fig. 2 A, B). The highest species richness in both sets of samples was observed near the Kara Strait, where the seafloor consists of mixed grounds offering a wide range of habitat types. A sparser benthic fauna found in the Pechora Bay and in the area around the Pechora river mouth reflects a benthic fauna which has to cope with low salinity (Remane and Schipper, 1971) and a strong seasonal variation in temperature and salinity (Adrov and Denisenko, 1996). The low species
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richness, abundance and biomass, found immediately outside the bay as well as in the other seas influenced by strong freshwater discharge (Denisenko et al., 1999), most probably reflect a quite uniform shallow water habitat of unstable sand, as is the case around the mouth of the Ob' Bay (Milliman and Syvitski, 1992; Lisitzin, 1995).

In general, the proportion of species from different systematic groups is similar in the Russian and Norwegian samples from the same stations. But at the stations 7 and 21, the number of species in the Russian samples was approximately 2/3 as compared to the findings of the Norwegian team. Small forms of crustaceans, such as Byblis gaimardi and Protomedia fasciata, and some species of echinoderms and polychaetes were not recorded in the Russian samples. These differences are attributed either to patchy occurrences of the organisms concerned, or to differences in sampling on stony or sandy sediments between the van Veen and "Ocean" grabs.

The environmental conditions, particularly bottom topography, sediment type, and water depth, strongly influence benthic community structure (Figs. 7, 8) as has been demonstrated for the study area (Dahle et al., 1998), which is not subjected to any significant anthropogenic impact (Loring et al., 1995).

The accumulation areas with high concentrations of total organic carbon (TOC) correlative to the fine fraction portion in bottom sediments (Klenova, 1960; Loring et al., 1995) are located in the Chernaya Fjord (St.11), Pomorskii Strait between Kolguev Island and the mainland (St.3), in the depression south of Novaya Zemlya (St. 7a, 8, 12-14), and near Dolgii Island (St. 24) (Loring et al., 1995). Surface and sub-surface deposit-feeding polychaetes are the most abundant faunal group in all these areas (Fig. 3 A, B). At station 29 located in the Pechora Bay, where TOC content is high, but salinity is very low, the deposit-feeding brackish-water bivalve Macoma balthica is the most abundant. Co-dominance of filter-feeding molluscs and bryozoans was observed in the nearshore zone (St. 21) and farther offshore at St. 7 located on the coarse grounds close to the Kara Gate Strait. This area is affected by strong bottom currents. Similar groups predominate at shallow St. 25 with water depth less than 15 m and strong water mixing. Like in the case with abundance, the biomass of polychaetes is the highest in organic-rich soft muddy sediments (St. 11, 12, 13) in the deepest northern part of the Pechora Sea. Polychaetes constitute the main part of the total biomass, because big molluscs with heavy shells, such as Tridonta borealis or Nicania montagui, are rare there.
Fig. 7. Cluster diagram showing station grouping based on the similarity of environmental data.

Fig. 8. Distribution of station groups according to their environmental characteristics (bottom sediments, depth, temperature, and salinity).
Key: 1 - estuarine shallow station; 2 - marine shallow stations with low TOC; 3 - marine stations with intermediate TOC; 4 - deep marine stations with high TOC.

An increase in coarse fraction portion leads to a change in the dominant group constituting the main part of the total biomass of zoobenthos, and detritivorous polychaetes are substituted by filter-feeding molluscs. At St. 6 and 7 on mixed grounds, the biomass of polychaetes is still quite high, but molluscs become more abundant compared to muddy sediments and, as a result, they dominate over polychaetes. Mobile and very large carnivorous animals, such as starfishes...
and crabs, are rarely caught by grab in the offshore area, but their occasional appearance can sometimes considerably increase the total biomass, as is the case with St. 6. It is an accidental fact, because biomass of echinoderms in the Pechora Sea does not usually exceed 50 g/m² (Khodkina, 1964).

The predominance in biomass of a detritovorous feeder, sea urchin Strongylocentrotus pallidus, at St. 21 on mixed grounds with low organic content is due to the presence of fine fraction in the surface sediment layer. The presence of diverse bryozoans, immobile filter-feeders with comparatively large biomass, testifies to the considerable portion of coarse fraction in the sediment of the area with good water exchange and high content of suspended organic matter in water column (Zenkevich, 1927).

As shown by Kuznetsov (1970), the trophic structure of fauna in a certain area is, in general, determined by a species, or several species with the same type of feeding, which have the biggest share in the total biomass of zoobenthos. Figures 7 and 8 show the four discrete groups of stations that differ from each other mainly in water depth and salinity. Group One occupies the areas deeper than 100 m, and Group Two occurs at the depths between 50 and 100 m. The stations of both groups are restricted to organic-rich sediments (Loring et al., 1995). Surface (Spirochaetopterus typicus, Macoma calcarea) and sub-surface (Maldane sarsi, Pectinaria hyperborea) deposit feeders predominate in Group One. Group Two is dominated by mobile filter-feeding species (Tridonta borealis, Nicaia montagui, Ciliatocardium ciliatum). Group Three includes shallow stations located at depths of 10-20 m. Suspension feeders, such as bivalve Serripes groenlandicus, bryozoans, and the ascidian Pelonaia corrugata predominate in the southern regions of the Pechora Sea and Kara Strait. A single station in the Pechora Bay forms Group Four, where deposit feeders predominate. In general, the bay represents a typical high latitude estuarine zone (Denisenko et al., 1999), where the distribution of abundance and biomass, as well as trophic structure, agree well with the generalized scheme for the whole Pechora Sea plotted on the basis of the data collected in 1992-1994 and the present data set (Denisenko et al., 1997).

As noted by Dahle et al. (1998), there are two main quantitative approaches to determine benthic communities or faunal associations. One approach mainly uses abundance (Petersen, 1913), whereas the other approach, usually adopted by Russian scientists, uses biomass or some other derivative (Moebius, 1877; Brodskaya and Zenkevich, 1939; Vorob'ev, 1949). The role of an organism in the transformation of matter and energy can be estimated knowing its respiration and production. Using the calculated production values reflecting the integrated data on abundance and biomass allows determining the functional role of each species in the community (Alimov, 1989; Brey, 1990; Denisenko and Denisenko, 1990). Owing to the use of production values, the importance of numerous small-bodied organisms and a single individual of a large-size species in the total production of a community can be compared and estimated. Thus, production characteristics allow statistically grouping samples collected throughout the year, including periods of mass juvenile recruitment. Comparison of the present results with previously published data (Zenkevich, 1927 in Dahle et al., 1998; Fig.6), which were based on analysis of biomass only, demonstrates a certain similarity in the structure of bottom communities of the Pechora Sea. The main
difference lies in a slightly reduced significance of large-size molluscs in the given outcome.

The present results show similar trends in community boundary determination to those outlined by Dahle et al. (1998), who used only numerical abundance in the faunal analyses. In both studies, a similar distribution pattern and similar dominant species were found in the areas subjected to environmental stress, such as the fjordic Chernaya Bay, the cold-water depression south of Novaya Zemlya, and the estuarine Pechora Bay. Opposite to this, in the open part of the Pechora Sea the dominant species of the communities determined with the use of production values differ markedly from those determined by abundance data only.

The reliability of the results in faunal groups analysis increases with growing number of stations and replications involved in the calculations. Thus, when the data of the present study are incorporated into larger-scale analyses (Denisenko et al., 1997), the minor difference is not unexpected. The distribution area of some communities determined during the present calculations was reduced, because some stations were included in the neighboring communities and integrated with them. It happened because in large-scale calculations significance for some species was decreased, while for other species it was increased. The last group of species is more regularly distributed as it is present in all investigated samples and replications.

Conclusions
Contrary to the existing opinion about sparse benthic fauna in the Pechora Sea resulting from long ice-covered period, insignificant Atlantic influence, and considerable freshwater runoff of the Pechora River (Zenkevich, 1927) the number of species appeared to be comparable with the number of species in the western Barents Sea (Brodkaya and Zenkevich, 1939). The present study supports previous investigations that have described plentiful sublittoral zoobenthos in this area (Denisenko et al., 1995; Antipova, 1975).

Trophic structure of zoobenthos, its biomass and abundance strongly depend on environmental conditions in the study area, as has been demonstrated by zoobenthos abundance in parallel data sets from the same cruise (Dahle et al., 1998).

Compared to the parallel data sets from the same stations analyzed using numerical abundance only (Dahle et al., 1998), the present study reveals differences in the species considered as dominant ones. However, in environmentally stressed areas, such as the Chernaya Bay and the depression south of Novaya Zemlya, where the dominant animals are relatively low in biomass, bottom communities were dominated by the same species.

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References


