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Diversity, distribution and ecology of benthic amphipods (Amphipoda, Gammaridea) in the Barents Sea sublittoral

ABSTRACT: In 1920 qualitative and quantitative benthos samples collected in Barents Sea sublittoral in the years 1951–1983 154 species, 77 genera and 30 families of Amphipoda Gammaridea were identified. Species diversity was highest among the Lysianassidae, Oedicerotidae, Ampeliscidae, Calliopiidae and Pleustidae. *Ampelisca eschrichti* clearly dominated the material. This same species, plus *Haploops setosa* and *Anonyx nugax* were both the most frequently occurring and most numerous species. The distribution of amphipods in the Barents Sea sublittoral varies both in diversity and numbers by region, depth, sediments and water temperature. Zoogeographical changes are discussed in the present paper. Altogether 331 species of amphipods have been hitherto collected in the Barents Sea, of which 317 species, 126 genera and 39 families belong to the suborder Gammaridea.

Key words: Arctic, Barents Sea, sublittoral, benthos, Amphipoda, Gammaridea.

Introduction

The Crustacea Malacostraca belong to the most numerous animal groups in Arctic Seas; among them the Amphipoda are especially diverse, with more than 519 species in the area (Tzvetkova 1995). Also in the Barents Sea the Amphipoda are among the most diverse animal groups: of almost 2300 species of benthic animals in this sea 14.2% are Amphipoda, although this is only one of 129 orders of animals present in the area (Bryazgin *et al.*, 1981).

Many amphipod species show a high ecological tolerance; this permits amphipod species to occupy various biotopes and to have a wide distribution both latitudinally and vertically. By their high abundance and biomass the amphipods are often among the dominant animal groups in the biocenoses. These crustaceans serve as an important food source for many fishes, seabirds and marine

invertebrates, and play an important role in the food web of the Barents Sea. Recently the important impact of amphipod predation on benthic eggs of marine fishes has also been elucidated (DeBlois and Leggett 1993).

An important peculiarity of the Amphipoda is the absence of pelagic larvae. The young develop in the marsupium and dispersal is therefore mainly by active dispersal of the adults. Amphipods are therefore a suitable group to use in zoogeographical studies, as was done in papers by *e.g.* Gurjanova (1951, 1975), Tzvetkova (1975) and Watling (1979).

The history of the study of amphipods in the Barents Sea region is more than 200 years old, but the first detailed surveys were prepared by Bulycheva (1947) and Gurjanova (1951). The collections of the Zoological Institute of the Russian Academy of Sciences, St.Petersburg, collected by different workers during 50 years, as well as all literature data from this period, form the databasis of those papers. Further intensive faunistic and taxonomic investigations of the Barents Sea were carried out in 1970–1980, and the list of amphipod species found in the area had increased by 16% (Tab. 1). For the updated taxonomy of species the catalogue of Palerud and Vader (1991) was used.

Table 1

Numbers of known species of Amphipoda in the Barents Sea region.

Authors	Amphipoda	Gammaridea
Bulytcheva 1947	268	254
Gurjanova 1951	276	262
Bulytcheva 1951, Oldevig 1959	280	286
Steele 1967, Steele and Brunel 1968, Bryazgin 1974a, b, c	307	293
Bryazgin *et al.* 1981	315	300
Bryazgin 1986, 1994	325	311

In the years 1980–1986 the fauna and ecology of the amphipods in the South Spitsbergen area (Węsławski 1990, Jażdżewski *et al.* 1995, Piepenburg *et al*, 1996, and others), and of the Pechora Sea (Anisimova and Lippova, 1996) were investigated.

The present paper focuses on a review of the diversity of the Amphipoda Gammaridea, often among the most frequent and numerous animals in bottom samples, and adds additional ecological and biological data from the period 1951–1983.

Material and methods

This study is based on material collected in various regions of the Barents Sea shelf (from 5–20 to 550 m) in the period from 1951 to 1983 and deals with *ca* 2000 samples (Tab. 2).

Table 2

The collected materials from the Barents Sea's sublittoral (the symbols see in the text).

Period	Research vessels	Trawl samples	Grab samples	Regions
1951-59	*Diana, Professor Derjugin* (MMBI)	278	250	SE Murman Coast
1968-70	*Vodnik, N.Maslov* (PRIMFO)	543	540	whole Barents Sea
1971	*Struja* (PRIMFO)	22	22	Murman Coast
1972	*Atlantida* (PRIMFO)	45	44	Lofoten area
1972	*Atlantida* (PRIMFO)	30	30	Kveytechol cavity, Beer Island area
1982	*Dalnije Zelentzy* (MMBI)	59	44	Svalbard, Bear Island
1983	*Dalnije Zelentzy* (MMBI)	13	0	Murman Coast
	Total	1920		

The main collections were gathered in 1968–1970 by the author, as part of a benthos survey of the Barents Sea sublittoral by the Polar Research Institute of marine Fisheries and Oceanography (PRIMFO) in Murmansk. This investigation covered the whole area from the coast to 78°30'N, from Novaya Zemlya to the Greenland deep, and from the southern Lofoten islands to Spitsbergen, thus practically all of the Barents Sea shelf area, except the shallowest sublittoral (Fig. 1).

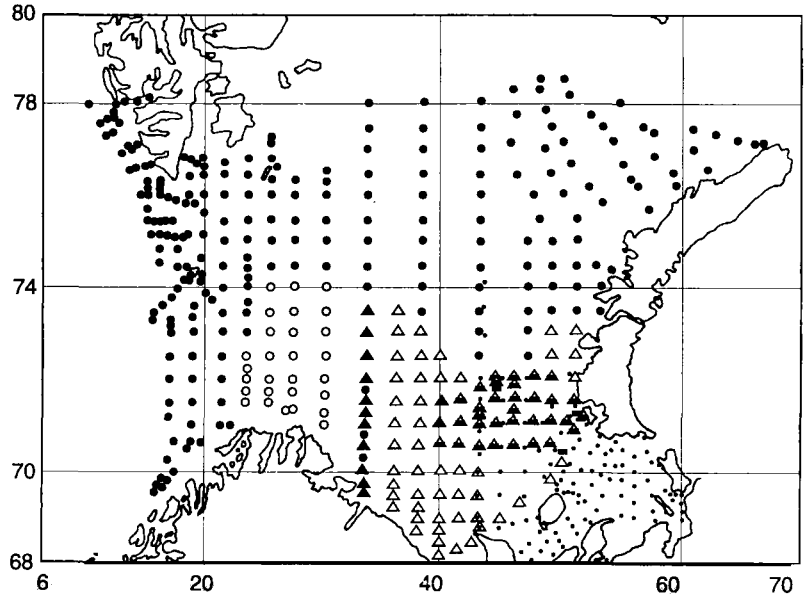

Fig. 1. Sublittoral benthos study area in Barents Sea in 1968–1970;
(open symbols – R/V *Vodnik*, closed symbols – r/v *N.Maslov*, triangles and white circles – 1968, black circles – 1969, black dots – 1970).

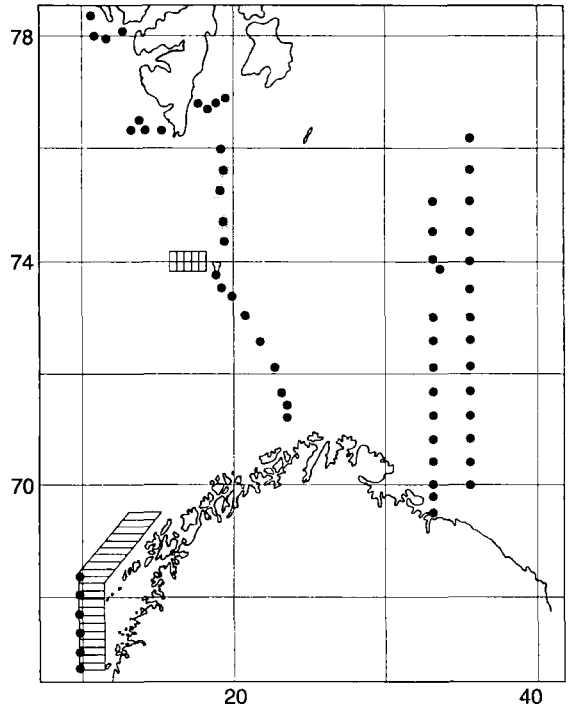

Fig. 2. Sublittoral benthos study area in Barents Sea in 1982 (r/v *Dalnije Zelentzy*).

Additional samples were collected by the Benthos Laboratory of the Murmansk Marine Biological Institute of the Russian Academy of Sciences (MMBI), collected by various specialists in 1951–1959 from the Murman coast areas and the southeastern part of the Barents Sea, and by the author in the years 1972–1983 in the western Barents Sea and the NE Norwegian Sea (Fig. 2).

The samples were taken with a Sigsby trawl (12 mm wide mesh) in 5-minute hauls, and by OKEAN-type grabs (0.25 squ.m.), with 2 or 3 replicates at each station. On deck, the samples were washed and sieved through a 0.5 mm screen and preserved in 4% buffered formalin solution. After 5–10 days the amphipods were sorted out and transferred to 70% alcohol.

After identification the amphipods were measured (body length, telson excepted, to the nearest 0.1 mm). Also the number and size (to the nearest 0.1 mm) of eggs were recorded. Amphipods were identified using the descriptions of Sars (1895), Stephensen (1935–1942), Gurjanova (1951, 1962), Barnard (1969), Barnard and Karaman (1991), and various more specialized papers.

An attempt to obtain quantitative information on amphipod distribution by means of the grab samples was unsuccessful because many nectobenthic amphipods are of large size and active swimmers, and therefore able to avoid the gear (Brandt *et al.*, 1996, author's own unpublished observations from deep-water

hydrostat). Therefore, all the bottom grab samples were only used for qualitative and faunistic data, and the biomass aspects were not studied further.

For a comparison of the zoogeographic distribution of the amphipods of the area, the shelf area was provisionally divided into 6 areas by the distribution patterns of the major zoogeographical groups of sublittoral amphipods in the Barents Sea (Bryazgin 1986), as follows:

SW – southwestern part, mainly Boreal area;
C – central part, transitional Boreal-Arctic area;
SE – southeastern part, mainly Boreal-Arctic area;
NE – northeastern part, manly Arctic area;
N – northern part, mainly High-Arctic area;
NW – northwestern part, mainly Arctic area (see Fig. 3).

Results

Composition and diversity of amphipod fauna

The collected material contains 154 species of Amphipoda Gammaridea, divided into 77 genera and 30 families (Tab. 3). Species diversity is highest in the Lysianassidae (12 genera, 32 species), the Oedicerotidae (10 and 15), the Ampeliscidae (3 and 15), the Calliopiidae (6 and 9), and the Pleustidae (6 and 9). The most abundant families are the Ampeliscidae (especially *Ampelisca eschrichti, Haploops laevis* and *H. setosa*) and the Lysianassidae (mostly *Anonyx nugax*). *Ampelisca eschrichti* is by far the most numerous and widespread amphipod in the Barents Sea sublittoral, very widespread are also *Haploops setosa, H. laevis, Anonyx nugax*, as well as *Epimeria loricata* and *Stegocephalus inflatus*; these species occur in the entire region. Also widely distributed are *Acanthonotozoma cristatum, Atylus smitti, Rhachotropis aculeata* and *Acanthostepheia malmgreni*; these amphipods are met with in at least 5 of the 6 regions, and occur as mass species in some of them.

More than 10 species predominate usually in the benthic samples, with species of the families Oedicerotidae, Calliopiidae, Eusiridae, Lysianassidae, Melitidae and Aoridae variously important in different regions. In small number of samples species with mainly intertidal or shallow-sublittoral distribution played a dominant role, such as representatives of the families Ampithoidae, Gammaridae, Isaeidae and Stenothoidae.

The species were divided into 6 categories of relative frequency following the system of Marques and Bellan-Santini (1993), with the following result: very common (>20%) – 0.7%, rather common (10–20%) – 0.7%, common (3–10%) – 10.9%, uncommon (1–3%) – 16.7%, rare (0.5–3%) – 9.4%, and very rare (<0.5%) – 61.6%.

Table 3

The list of the gammaridean families in the Barents Sea.

No	Families	Total of the sea		In collections	
		genus	species	genus	species
1	Acanthonotozomatidae	1	8	1	5
2	Amathillopsidae	1	2	–	–
3	Ampeliscidae	3	17	3	15
4	Amphilochidae	4	7	–	–
5	Ampithoidae	1	1	1	1
6	Anisogammaridae	1	1	1	1
7	Aoridae	4	8	3	7
8	Argissidae	1	1	1	1
9	Astyridae	1	1	–	–
10	Atylidae	1	5	1	3
11	Calliopiidae	9	17	6	9
12	Corophiidae	3	5	1	1
13	Dexaminidae	1	1	–	–
14	Epimeriidae	2	4	2	2
15	Eusiridae	2	7	2	5
16	Gammaracanthidae	1	1	1	1
17	Gammarellidae	1	1	1	1
18	Gammaridae	2	12	2	3
19	Hyalidae	1	1	–	–
20	Iphimediidae	1	1	–	–
21	Isaeidae	3	8	2	4
22	Ischyroceridae	3	13	2	7
23	Lafystiidae	1	1	–	–
24	Leucothoidae	1	1	1	1
25	Lilljeborgiidae	2	3	2	3
26	Lysianassidae	26	81	12	32
27	Melitidae	3	8	3	8
28	Melphidippidae	1	2	–	–
29	Odiidae	1	1	–	–
30	Oedicerotidae	12	32	10	15
31	Pardaliscidae	2	4	2	4
32	Phoxocephalidae	3	6	2	4
33	Pleustidae	6	13	6	9
34	Podoceridae	4	9	1	1
35	Pontoporeiidae	4	4	2	3
36	Stegocephalidae	5	5	2	2
37	Stenothoidae	5	22	1	3
38	Synopiidae	2	2	2	2
39	Urothoidae	1	1	1	1
	Total	126	317	77	164

Ecological terms for distributions

The distribution of amphipods in the sublittoral Barents Sea is not uniform, but varies with region, depth, temperature and sediments (Tab. 4, Fig. 3). Mean frequency of occurrence of amphipods is 66.5%, the highest frequency occurred in the Petchora Sea (the region between Kolguev, Novaja Zemlja and the Vaygach islands), with 98.2%, the lowest in the SW and N regions, only 18–20% (Bryazgin 1986, 1994 and present data). The distribution of the amphipods in the area is extremely irregular: 17 and 18 species, respectively, were found in the N and NE region, 42 and 51 spp. in the SW and C regions, and 64 in the NW region. The highest number, 123 species, was collected in the SE region. Thus, species diversity is highest in the shallow Petchora Sea, along the south coast of Novaja Zemlja and in the western region, at depths of *ca* 50 m.

Of 154 species of Gammaridea 118 (76.6%) were collected in depths shallower than 100 m, and only 36 (23.4%) were found below 100 m. 74 species (48.0%) preferred the shallowest 50 m. Only 29 species (18.8%) were found living deeper than 400 m; while 14 species (9.1%) were not found in depths shallower than 200 m.

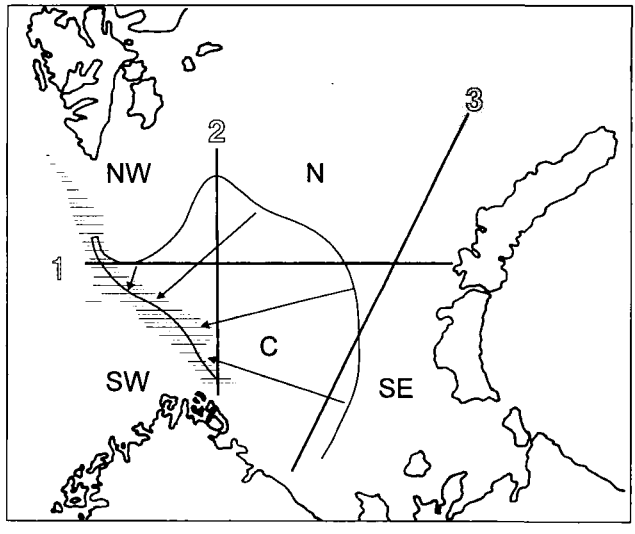

Fig. 3. Tentative zoogeographical division of the Barents Sea sublittoral based on the distributions of amphipods; Transect 1: by 74°N; 2 – by 28°E; 3 – Murman coast (Semiostrovje) – Franz-Josef Land. Symbols as in text. Shaded area – common occurrence of Arctic and Boreal species in coldwater period 1968–1970.

Frequency of occurrence of the more numerous species in the different regions is given in Table 5. It seems clear that their quantitative distribution is roughly similar to that of the amphipods as a whole. Among the 14 most abundant species only one, *Haploops setosa*, is often found at depths below

Table 4

The list of gammaridean species collected in the sublittoral of the Barents Sea in 1951–1983
(cl – clay, gr – gravel, r – rock, sa – sand, sh – shells, si – silt, st – stones).

Species	F.o. %	Regions						Depth m	Temp. °C		Bottom	Body length, mm		Eggs		
		SW	C	SE	NE	N	NW		from	to		male	female	Oviger.	No.	D, mm
Acantonotozomatidae																
Acantonotozoma cristatum (Ross, 1835)	0.37	+	+		+	+	+	40-250		3.1	cl,si,st	27.0	30.0	VI,X		
A. inflatum (Kröyer, 1842)	0.73			+				55-100	0.6	4.3	sa,st,gr,sh		16.0	VI		
A. cf. *magnum* Just, 1978	0.10			+				49-82		0.3	si,sa		4.0			
A. rusanovae Bryazgin, 1974	0.37	+			+		+	50-148	0.7	1.7	r,st,sh		10.0	VI-IX		
A. serratum (Fabricius, 1780)	0.55	+	+	+			+	20-350	0.4	3.6	r,st,sh	9.0	10.0	IX	17	0.4
Ampeliscidae																
Ampelisca aequicornis Bruzelius, 1859	0.18	+						10-310		2.1	si,sa		12.0	VI	10	0.9
A. eschrichti Kröyer, 1842	26.90	+	+	+	+	+	+	22-460	-1.6	2.3	si	32.0	35.0	VI-XI	32	2.5
A. macrocephala Liljeborg, 1852	4.03	+	+	+			+	13-440	-0.4	3.4	si,sa,cl		29.0	VI-VIII		
A. odontoplax Sars, 1895	1.10	+						255-310	2.1	6.6	si,sa,st		22.0	VI	10	1.7
A. spinipes Boeck, 1860	0.18	+						190-310	2.1	6.6	si,sa,st	11.0	16.0			
Byblis affinis Sars, 1891	1.10	+	+	+				80-300	1.1	6.6	si,sa,gr,st		18.0	VI		0.8
B. erythrops Sars, 1883	1.10		+	+				40-185	-0.4	2.1	cl,si,gr,st	21.0	17.0	VIII		
B. gaimardi (Kröyer, 1846	7.32	+	+	+			+	14-360	-1.5	4.9	cl,si,sa	17.0	20.0	I-XII	47	1.1
B. longicornis Sars, 1891	1.48			+				48-415	-1.7	3.1	cl,si,st		22.0	VI-VIII		1.2
B. minuticornis Sars, 1879	0.18	+						80-480		1.4	si,st		8.0			
Haploops laevis Hoek, 1882	9.88	+	+	+	+	+	+	23-265	-1.8	5.0	si,cl	18.0	19.0	VIII-IX		0.8
H. setosa Boeck, 1871 + *H. robusta* Sars, 1891	11.71	+	+	+			+	80-525	-1.0	6.6	si,sa,st	22.0	23.0	VI,VIII,XII	34	1.3
H. sibirica Gurjanova, 1909	0.37						+	22-77	-1.1	1.7	sa,si,st		20.0			
H. similis Stephensen, 1925	1.10	+	+					80-500	1.0	2.7	si,cl,st		7.0			
H. tubicola Liljeborg, 1855	6.22	+	+	+	+	+	+	22-480	-1.8	4.0	si,cl,st	11.0	18.0	III,VIII,XII	56	1.1
Ampithoidae																
Ampithoe rubricata (Montagu, 1808)				+				5					11.0			
Anisogammaridae																
Anisogammarus macginitiei Shoemaker, 1955	0.18			+				140	-1.8				14.0			
Aoridae																
Arctolembos arcticus (Hansen, 1887)	4.03			+				14-205	-1.5	1.6	cl,sa,si	35.0	34.0	VIII	12	3.0

Table 4 – *continued.*

Autonoe longipes (Liljeborg, 1852)	0.18	+		+				5.0								
A. megacheir Sars, 1879	0.18			+				82		1.5	ci,sa	9.0				
Leptocheirus sp.				+												
Unciola laticornis Hansen, 1887	0.37		+					500	2.2	2.7	si,cl,st		13.0			
U. leucopis (Kröyer, 1845)	2.75	+	+	+			+	70-400	-1.1	4.1	si,cl,sa		17.0	VI-IX	35	0.6
U. planipes Norman, 1867	0.18			+				60		5.4	sa,sh		6.0	VIII	5	0.4
Argissidae																
Argissa hamatipes (Norman, 1869)	0.18		+	+				25		-0.4	si,cl		6.0			
Atylidae																
Atylus carinatus (Fabricius, 1793)	0.37		+	+			+	6-14	-0.6	7.6	cl,sa	25.0	32.0	VIII		
A. nordlandicus Boeck, 1871	0.37	+	+	+				170-300	1.7	3.8	si,sa,st		7.0			
A. smitti (Goës, 1866)	2.01		+	+	+	+		58-230	-1.6	1.0	si,st,cl,sa	28.0	32.0	IX,X	59	1.5
Calliopiidae																
Amphithopsis longicaudata Boeck, 1861	0.10		+					185		1.5	st		5.5			
Apherusa jurinei (Milne-Edwards, 1830)	0.18			+				16-19		-0.2	cl		10.0	VIII		
A. sarsi Schoemaker, 1930	0.18			+			+	55		-0.6	sh,st		12.0	VIII		
A. tridentata (Bruzelius, 1859)	0.18			+				6		13.4	st	13.0	16.0	VIII		
Calliopius laeviusculus (Kröyer, 1838)	0.37	+	+				+	60					16.0			
Halirages fulvocincta (M. Sars, 1858)	0.92		+				+	45-350	-1.7	4.9	si,sa,st		19.0	VIII,XI		
H. quadridentata Sars, 1876	0.92		+	+				8-500	-1.4	5.4	si,sa,st		27.0	VIII,X		
Leptamphopus sarsi Vanhöffen, 1897	0.18		+					145		3.0	si,sa,cl		5.0	VI		
Rozinante fragilis (Goës, 1866)	0.37			+	+		+						22.0			
Corophiidae																
Neohela monstrosa (Boeck, 1861)	1.10	+	+	+			+	80-525	1.4	3.9	si,sa,st	36.0	32.0	IV,VIII		
Epimeriidae																
Epimeria loricata Sars, 1879	3.29	+	+	+	+	+	+	75-525	1.1	4.1	si,st,sh,gr	24.0	28.0	III,VIII-XI	20	2.2
Paramphithoe cuspidata (Lepechin, 1780)	2.01			+			+	48-300	0.4	4.3	st,sa,sh	27.0	24.0	VII,IX,X		
Eusiridae																
Eusirus cuspidatus Kröyer, 1845	2.01		+	+			+	18-80	-0.8	9.2	st,sa,sh	25.0	28.0	X	17	2.8
E. propinquus Sars, 1893	0.18		+					180		2.4			22.0			
Rhachotropis aculeata (Lepechin, 1780)	8.24	+	+	+		+	+	30-525	-1.5	4.3	cl,si,sa,st	20.0	30.0	IV,VI,X	139	1.2
R. inflata (Sars, 1882)	0.18		+					300		2.4	st		8.0			

Table 4 – *continued.*

R. helleri (Boeck, 1871)	0.37	+	+					310-370	1.2	3.6	st,sa,cl		20.0	VIII,IX	2.5	
Gammaracanthidae																
Gammaracanthus loricatus (Sabine, 1821)				+				10		10.6	sa,si		36.0	VIII	383	0.6
Gammarellidae																
Gammarellus homari (Fabricius, 1779)				+				41			sh,sa,si		13.0			
Gammaridae																
Weyprechtia heuglini (Buchholtz, 1874)	0.92			+	+	+	+	15-52	-1.1	1.6	sa,cl	32.0	46.0	VIII		
W. pinguis (Kröyer, 1838)				+			+	2-50								
Isaeidae																
Goesia depressa (Goës, 1866)	0.37		+	+				50-90		1.2	st,cl		12.0	IX		
Photis reinhardi Kröyer, 1842	0.55	+		+				14-80	-0.6	1.0	cl,sa,st,si		6.0	VIII	4(?)	0.5
Protomedeia fasciata Kröyer, 1842	0.18		+	+			+	46		6.3			6.0	VII		
P. grandimana Brüggen, 1905	0.18		+	+			+	10-49		4.9	sa,sh,st		9.0	VII,VIII		
Ischyroceridae																
Ericthonius difformis Milne-Edwards, 1820				+												
E. megalops (Sars, 1879)	0.37		+					125-260	2.4	3.2	si,sa,st,sh		8.0	VII		
Ischyroceros assimilis Sars, 1879	0.18			+				170-500	-1.8	2.2	si,gr,st		7.0			
I. enigmaticus Gurjanova, 1934	0.37		+	+			+	6-110	-0.2	13.4	si,gr,st	10.0	11.0	VIII		
I. latipes Kröyer, 1842	0.92			+				10-60	-0.6	6.3	cl,sa,sh	13.0	15.0	VIII		
I. megacheir (Boeck, 1871)	0.37	+	+				+	200-500	0.4	2.2	si,st,r,gr	10.0	15.0	VIII,IX	14	0.3
I. nanoides (Hansen, 1887)	0.09		+					480								
Leucothoidae																
Leucothoe spinicarpa (Abildgaard, 1789)	0.18	+		+				83-510		5.2	gr,st	12.0	13.0	VIII		1.5
Lilljeborgidae																
Idunella aequicornis (Sars, 1876)	0.37			+				130-255	0.7	3.0	si,sa		10.0	IX,X	5	0.6
Lilljeborgia fissicornis (M.Sars, 1858)	1.10	+	+	+			+	128-330	0.4	3.3	sa,si,st		25.0	VI-IX		
Lilljeborgia sp.				+				53			st		5.0	X	0.5	
Lysianassidae																
Anonyx compactus Gurjanova, 1962	0.18			+				12		-1.1	sa		18.0			
A. laticoxae Gurjanova, 1962	0.18						+	30		3.0	st,sh		30.0	IX		
A. lilljeborgi Boeck, 1870	1.83			+	+		+	30-290	-0.1	6.3	sa,sh,gr	15.0	18.0	VIII		
A. nugax (Phipps, 1774)	9.52	+	+	+	+	+	+	12-400	-1.8	6.3	cl,si,sa,st	42.0	46.0	VI-XI	65	2.7

Table 4 – *continued.*

A. sarsi Steele *et* Brunel, 1960	2.01			+	+	+	+	46-280	-1.8	6.3	sa,st,sh,si	26.0	25.0	VIII,IX		
Aristias topsenti Chevreux, 1900	0.18	+						500		2.2	s,st		3.5			
A. tumidus (Kröyer, 1846)	0.18						+	200		0.4	r		10.0			
Centromedon productus Goës, 1866	0.75				+		+	100-155		-1.8	cl,si		12.0	IX	8	0.7
C. pumilus (Lilljeborg, 1865)	0.18	+					+	100-156		-1.6	si,st,cl		10.0	IX	8	1.1
Hippomedon holbolli (Kröyer, 1846)	1.10	+	+	+			+	80-310	-1.1	3.3	si,sa	17.0	18.0	VI		
H. propinquus petschoricus Bryazgin, 1977	0.18			+				23		-1.0	cl		11.0	VIII		
Lepidepecreum umbo (Goës, 1866)	1.28		+				+	210-440	-1.8	-0.2	st,sa,cl		13.0	IX	36	0.8
Menigrates maslovi Bryazgin, 1974	0.03	+	+					80-215		3.5	si,st	13.0	14.0	VIII		1.6
M. obtusifrons (Boeck, 1861)	0.18			+			+	48-193		1.1	cl		13.0			
Onisimus brevicaudatus Hansen, 1886	0.55				+		+	103-230	-1.8	0.2	si,st		17.0	VIII,IX	14	1.2
O. edwardsi (Kröyer, 1846)	0.55			+		+	+	30-70	-0.6	1.2	sa,st,sh		14.0			
O. krassini Gurjanova, 1951	0.18			+				94		-1.0	cl,si		13.0	VIII		
O. litoralis (Kröyer, 1845)		+	+	+			+	pelagic					16.0			
O. normani (Sars, 1895)	0.18	+	+	+				275		3.7	st,si		6.0	VI		
O. plautus (Kröyer, 1845)	1.81	+	+	+				14-230	-1.0	3.0	cl,si,st	1.0	11.0	VI,VIII	7	1.0
O. sirius Gurjanova, 1962	0.18						+	100		-1.8	si		9.0	IX	9	1.0
Orchomene macroserratus Shoemaker, 1930	0.18			+				30-40		-1.4	si		9.0			
O. serratus (Boeck, 1861)	0.37	+	+					190-500	2.2	6.6	st,si		8.0	VIII		0.6
O. tschernyschevi Brüggen, 1909	0.18						+	70		1.0	gr,sh		7.0	VIII	15	0.7
Orchomenella lepidula Gurjanova, 1962	1.10			+			+	23-155	-1.5	1.2	cl,si,sa	7.0	7.0	VIII,IX	6	1.0
O. minuta (Kröyer, 1846)	0.37			+			+	40-52	-0.1	1.6			14.0	VIII		
Socarnes bidenticulatus (Bate, 1835)	0.55				+		+	80-180	-1.8		cl,si	27.0	31.0	VII-IX	63	1.9
S. vahlii (Kröyer, 1838)	0.18		+	+				6-200			st,gr,sa		15.0			
Tmetonyx cicada (Fabricius, 1780)	2.38			+	+		+	80-440	1.2	4.1	si,st,sa	21.0	26.0	VIII,IX	26	1.5
T. coeculus (Sars, 1891)	0.18	+						480			st,si	8.0				
T. similis (Sars, 1891)	0.37	+	+	+				55-500	-0.6	2.2	si,gr,st		20.0	IX	13	1.4
Tryphosella abyssalis (Stephensen, 1925)	18					+		30			st,gr		6.5	VIII		0.5
Melitidae																
Ceradocus torelli (Goës, 1866)	0.09			+				125			fish		48.0	IX		
Maera loveni (Bruzelius, 1859)	0.55		+	+				54-265		4.6	cl,sa,sh	34.0	35.0	VIII,IX		
M. prionochira Brüggen, 1907	0.09			+				2-50								
Melita dentata (Kröyer, 1842)	4.94			+	+	+	+	24-190	-1.1	9.0	sa,cl,st	27.0	21.0	VIII,IX		

Table 4 – *continued.*

M. formosa Murdoch, 1866	2.01		+	+				34-430	-1.5	3.5	cl,sa	24.0	21.0	VI-VIII		
M. palmata (Montagu, 1804)	0.37			+				52-55	0.6	1.6	cl		16.0	VI-VIII	65	0.9
M. quadrispinosa Vosseler, 1889	1.10		+	+			+	63-240	-1.5	4.4	cl,si,st,sa	11.0	13.0	VIII		
Melita sp.								62								
Oedicerotidae																
Acanthostepheia behringiensis (Lockington, 1877)	3.84		+	+				6-150	-1.2	9.9	sa,cl,si	26.0	29.0	VIII-X	90	1.1
A. malmgreni (Goës, 1866)	4.03		+	+	+	+	+	12-360	-1.5	4.9	sa,cl	31.0	29.0	VIII-X	38	1.4
Aceroides latipes Sars, 1866				+				200-250	1.1	2.0	si,sa		7.0			
Arrhinopsis longicornis Stappers, 1911				+				40		4.2	sa,st,gr		2.0			
Arrhis phyllonyx arcticus Bryazgin, 1974	3.84	+	+	+		+	+	22-450	-1.4	3.1	si	20.0	20.0	VIII-X		0.7
Bathymedon obtusifrons (Hansen, 1888)				+						4.5						
Monoculodes borealis Boeck, 1871	0.73			+			+	30-300	0.3	7.7	sa,st,si,cl		10.0			
M. latimanus (Goës, 1866)				+				53			st		7.0			
M. norvegicus (Boeck, 1861)				+									7.0			
Monoculopsis longicornis (Boeck, 1871)	0.09			+				75	0.5		si,sa		4.0			
Oediceros borealis Boeck, 1871				+				96			sa,cl		9.0			
Paroediceros lynceus (M.Sars, 1858)	2.20		+	+			+	14-250	-1.0	4.1	sa,st	21.0	23.0	IV,VII,VIII		
P. propinquus (Goës, 1866)	0.37			+				125	0.4	1.0	si,cl,gr,st		1.5	IX		1.1
Westwoodilla brevicalcar (Goës, 1866)	0.18			+				102			sa,si,sh,st		6.0			
W. caecula (Bate, 1856)	0.18			+									7.0	IX		0.5
Pardaliscidae																
Halice abyssi Boeck, 1871	0.18	+						500	2.2		st,si		17.0			
Pardalisca abyssi Boeck, 1871	0.37	+						300-330	3.1	5.9	sa,st,si		30.0			
P. cuspidata Kröyer, 1842	2.01			+			+	42-198	-1.3	2.9	st,sh.r		15.0	VI,VII,X	20	1.1
P. tenuipes Sars, 1893	0.18	+						500		2.7	si		9.0			
Phoxocephalidae																
Harpinia antennaria Meinert, 1890	0.18		+	+				125-500	2.2	3.2	sa,si,st,gr		5.5	VII,X	8	0.5
H. mucronata Sars, 1879	0.09			+			+	200		3.2	si,sa,st		4.0	X		0.5
H. pectinata Sars, 1891	0.09			+				75	0.3	0.5	si,sa		5.5			
Paraphoxus oculatus (Sars, 1879)	0.18			+				185-280	1.0	3.2	si,cl	5.0	5.0	X	5	0.5
Pleustidae																
Neopleustes pulchellus (Kröyer, 1846)	0.37			+				67-150					21.0	IV		

Table 4 – *continued.*

N. euacanthus (Sars, 1876)	0.18			+			+	55		0.6			12.0			
Parapleustes assimilis (Sars, 1882)	0.18			+				79-180		-1.9	si,cl		6.0			
P. bicuspis (Kröyer, 1838)	0.92			+			+	20-350	0.7	7.3			10.0			
Pleustes panopla (Kröyer, 1838)	0.18			+			+	83-420		1.8			15.0			
P. tuberculata Bate, 1858	1.10		+	+			+	14-420	-1.0	2.0	cl,sa		22.0	VI-VIII	17	1.4
Pleustomesus medius (Goës, 1866)	0.37			+			+	115-205	2.0	3.5			7.5			
Pleusymtes pulchella (Sars, 1876)	0.37			+				150-255	-0.5	1.7	si,sa		7.0	IX		
Stenopleustes latipes (M. Sars, 1858)	0.18			+				100-200		0.4			12.0	IX	10	0.5
Podoceridae																
Dulichia spinosissima Kröyer, 1845	0.37	+	+	+				68-80		-1.6		22.0	23.0			
Pontoporeiidae																
Monoporeia affinis (Lindstrom, 1855)	0.18			+				6		13.4	sa,si		7.0			
P. femorata Kröyer, 1842	1.81			+			+	7-225	-1.8	10.2	sa,si,gr,sh		7.5			
Priscillina armata (Boeck, 1861)	0.18			+				8-187	7.5	8.5	si,sa		8.0			
Stegocephalidae																
Phippsiella similis (Sars, 1891)	0.18		+				+	300		0.4	st,r		7.0			
Stegocephalus inflatus Kröyer, 1841	6.04	+	+	+	+	+	+	30-380	-1.8	2.4	st,cl,sa		38.0	IV,V,IX,X	76	1.6
Stenothoidae																
Metopa borealis Sars, 1882	0.18			+				40		4.4	si,sa,gr,st		2.5			
M. norvegica (Liljeborg, 1851)	0.18			+				97-190		2.7	sa,si,sh		6.5	X	17	0.5
M. pusilla Sars, 1982	0.18			+				180		-1.9	si,cl		3.5	IX		
Synopiidae																
Syrrhoe crenulata Goës, 1866	0.92			+			+	55-500	-0.6	3.6	st,sa,si,gr	10.0	10.5	VIII-X		0.9
Tiron spiniferum (Stimpson, 1853)	0.37			+			+	80-185	1.7	3.0	sh,st		6.0	VIII		
Urothoidae																
Urothoe elegans (Bate, 1856)	0.37	+		+				125-225	2.0	2.4	si,sa,sh,gr		4.5	X		

250 m, in the western parts of the area. The optimal depth range for the other 13 species is 50–100 m, and they occur most frequently in the SE region, particularly in the Petchora Sea.

As to sediment preferences, 94% were collected on soft bottoms (40% on silt, 20% on sand-silt, 14.4% on stones-silt, and 19.5% on clay), and only 6% on hard bottoms (rock, gravel and shells).

Table 5

Frequency of occurrence (%) of the common species of Amphipoda in the Barents Sea sublittoral (areas as in Fig. 3).

Species	Preference		SW	NW	C	SE	NE	N	Barents Sea
	depth m	t °C							
Anonyx nugax	50-100	-1.2 ~ 0.5	1.4	7.0	8.1	12.1	6.6	6.3	9.52
Stegocephalus inflatus	80-150	-1.0 ~ 0.5	1.4	6.0	4.2	6.8	13.3	1.3	6.04
Ampelisca eschrichti	50-100	-1.6 ~ 0.5	17.1	20.0	24.6	34.0	12.0	9.3	26.90
A. macrocephala	30-50	-0.4 ~ 3.4	4.3	3.0	3.0	3.1	0	0	4.03
Byblis gaimardi	14-300	-0.5 ~ 1.5	1.3	3.0	4.3	7.8	0	0	7.32
Haploops laevis	50-100	-1.8 ~ 1.0	2.8	3.0	7.1	13.7	10.6	9.3	9.88
H. setosa	250-300	1.5 ~ 2.7	45.7	20.0	10.6	11.0	0	0	11.71
H. tubicola	80-480	-1.5 ~ 2.0	7.1	11.0	6.8	5.1	2.6	1.3	6.22
Acanthostepheia behringiensis	10-50	-1.2 ~ 1.0	0	0	1.3	2.6	0	0	3.84
A. malmgreni	50-100	-1.5 ~ 1.0	0	2.0	6.8	6.3	4.0	2.8	4.03
Arrhis phyllonyx arcticus	50-100	-1.5 ~ 1.0	2.8	5.0	3.2	1.6	0	0.3	3.84
Rhachoropis aculeata	50-100	-0.5 ~ 2.5	5.7	18.0	5.2	4.7	0	4.3	8.24
Melita dentata	25-50	0.5	2.0	3.0	4.1	5.2	1.3	1.3	4.98
Lembos arcticus	20-50	-1.5 ~ 0.5	0	0	0	1.6	0	0	4.03

Amphipods were registered at temperatures between -1.8 to 13.4°C. The highest temperatures were observed in the shallow water of the Cheskaya Inlet (SE) during summer. We found 74 species at temp. of -1.8 to 0.5°, 25 species at temp. of 0.5 to 1.5°, 36 species at temp. of 1.5 to 2.5°, 22 species at temp. of 2.5 to 3.5°, 18 species at temp. of 3.5 to 4.5°, 9 species at temp. of 4.5 to 5.5°, and only 6 species at temp. higher than 7.5°C. The bulk of the Barents Sea amphipods consists of stenothermal species that are found at a temperature range of -1.8 to 3.5°C (Tab. 5).

Discussion

Composition

On the base of the numerous literature data and the present investigations the list of Amphipoda Gammaridea of the Barents Sea consists of 331 species, of which 317 are Gammaridea (Tab. 3). This is a large number, compared to the

other Arctic seas. Of the 519 amphipod species (in 167 genera and 45 families) listed by Tzvetkova (1995) 61% (75.5 of genera, 87% of families) are living in the Barents Sea. Also the list of dominant families in the Arctic is very similar to that of the Barents Sea; most diverse are the Lysianassidae (26 genera, 81 species), the Oedicerotidae (12–32), the Stenothoidae (5–22), the Ampeliscidae (3–17), the Calliopiidae (9–17) and the Pleustidae (6–13). This further confirms the strong Arctic character of the Barents Sea amphipod fauna.

A comparison of the amphipod fauna with the other Arctic seas shows, not surprisingly, that the similarity is greatest with the Kara Sea, with 79% species in common. There is also a high similarity with the faunas of the White Sea (62.4%), the Franz-Josef Land area (61.6%), and the East Greenland area (60.0%). Moving eastwards, the similarity gradually decreases, from 68% in the Laptev Sea to 24% in the Japan Sea.

Zoogeography

A zoogeographical analysis of the Barents Sea amphipod fauna showed that the Gammaridea as a whole prevalently were of Boreo-Arctic (38.9%) and Arctic (23.1%) affinities (Bryazgin 1994). Also Boreal species are common; together with Amphiboreal they make up 22.8% of the fauna. It should be pointed out that analysis took into account littoral as well as sublittoral species. The long-term structure of the amphipod fauna of the Barents Sea is not constant, and depends mainly on sea temperature changes. Such changes mainly depend on fluctuations of solar activity (with a "frequency" of 89–90 years, although cycles with a shorter "frequency" clearly also play an important role). The changes in the fauna as the result of these long-term oscillations do not only result in displacement of the boundaries between Arctic and Boreal species, but also result in changes in general productivity of the sea. Some species disappear as the result of the warming or cooling of the area, others decrease strongly but maintain some footholds, while still others greatly increase in numbers. Such changes can be noticed in all segments of the fauna – plankton as well as benthos, invertebrates as well as fishes.

It has been well established, that the Barents Sea, after a long, quite warm period of 20–50 years, now is undergoing a cooling trend. The first indications of this new cooling cycle were based on analyses of the bottom fauna in the southwestern Barents Sea and the waters south west of Spitsbergen, as studied by Nesis (1960), Blacker (1965) and Vader (1971), and on analyses based on the material from the entire area (collected in the years 1968–1970, see Fig. 1, by Bryazgin 1974a,b,c; Antipova 1975, Galkin 1976, and others).

The biogeographic structure of the Barents Sea sublittoral, based on material collected in the period 1951–1983 is dominated by Boreo-Arctic species, constituting 57.8% of the fauna (Tab. 6). In the southwestern part of the area the share of Arctic-Boreal species (81.0%) is especially high, compared to all other regions;

Table 6

Zoogeographical composition of Amphipoda in the Barents Sea sublittoral; n – number of species; regions as in Fig. 3.

Zoogeographical groups / Regions	SW		C		SE		NE		N		NW		Total	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Arctic	**0**	**0**	**1**	**2.0**	**3**	**2.4**	**1**	**5.9**	**1**	**5.9**	**2**	**3.2**	**7**	**4.5**
High-Boreal Arctic	**3**	**7.1**	**18**	**35.3**	**31**	**25.3**	**6**	**33.3**	**4**	**23.6**	**21**	**32.8**	**44**	**28.6**
Atlantic, Arctic, Pacific	0	0	5	9.8	6	4.9	1	5.6	1	5.9	6	9.4	10	6.5
Atlantic, Arctic	3	7.1	8	15.7	12	9.8	2	11.1	1	5.9	7	10.9	18	1.7
Arctic, Pacific	0	0	5	9.8	13	10.6	3	16.6	2	11.8	8	12.5	16	10.4
Boreal Arctic	**34**	**81.0**	**32**	**62.7**	**84**	**68.3**	**11**	**61.1**	**12**	**70.5**	**41**	**64.0**	**89**	**57.8**
Atlantic, Arctic, Pacific	17	40.5	20	39.1	43	35.0	10	55.5	9	52.9	26	40.6	46	29.9
Atlantic, Arctic	17	40.5	11	21.6	39	31.7	1	5.6	3	17.6	13	20.3	39	25.3
Arctic, Pacific	0	0	1	2.0	2	1.6	0	0	0	0	2	3.1	4	2.6
High-Boreal	**1**	**2.4**	**0**	**0**	**3**	**2.4**	**0**	**0**	**0**	**0**	**0**	**0**	**3**	**2.1**
Atlantic, Pacific	1	2.4	0	0	1	0.8	0	0	0	0	0	0	1	0.7
Atlantic	0	0	0	0	2	1.6	0	0	0	0	0	0	2	1.4
Boreal	**4**	**9.5**	**0**	**0**	**2**	**1.6**	**0**	**0**	**0**	**0**	**0**	**0**	**6**	**3.8**
Atlantic, Pacific	1	2.4	0	0	2	1.6	0	0	0	0	0	0	3	1.9
Atlantic	3	7.1	0	0	0	0	0	0	0	0	0	0	3	1.9
Not classified													5	3.2
Total	**42**	**27.3**	**51**	**33.1**	**123**	**79.9**	**18**	**11.7**	**17**	**1.0**	**64**	**41.6**	**154**	**100**

in this area also the share of Boreal species is noticeable (9.5%), and the number of High-Boreal Arctic species (7.1%) the lowest in the area. The opposite situation pertains to the northeastern region: fewest Boreal Arctic species, a complete absence of Boreal species, and the greatest share of Arctic and High-Arctic species (39.2%). Compared to a long term mean, the period 1951–1983 in the Barents Sea in the sublittoral is characterized by a gradual increase of the coldwater species and a reduction of the number of Boreal species.

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Streszczenie

W materiałach zgromadzonych w latach 1951–1983 przez autora i innych badaczy Morza Barentsa z murmańskich instytucji naukowych (PRIMFO i MMBI) stwierdzono 154 gatunki Amphipoda Gammaridea należących do 77 rodzajów reprezentujących 30 rodzin obunogów. Zdecydowanie dominującymi gatunkami pod względem częstości występowania i liczebności były *Ampelisca eschrichti, Haploops setosa* (Ampliscidae) oraz *Anonyx nugax* (Lysianassidae). Szczegółowe dane dotyczące występowania stwierdzonych gatunków Amphipoda (zakres głębokości, temperatury, płodności, wielkości maksymalnej samic i samców oraz ich kwalifikację zoogeograficzną znaleźć można w obszernej Tabeli 4.