

Global distribution patterns of genera occurring in the Arctic Ocean deeper 2000 m

A.N. Mironov, A.B. Dilman, E.M. Krylova

P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky Pr., 36, Moscow, 117997, Russia; e-mail: miron@ocean.ru

ABSTRACT: A list of genera represented in the abyssal (>2000 m) of the Arctic Ocean was compiled for 8 classes (Scaphopoda, Bivalvia, Crinoidea, Echinoidea, Holothuroidea, Asteroidea, Ophiuroidea and Ascidiacea) and some orders from the classes Anthozoa, Maxillopoda and Malacostraca. This list includes 92 genera and 133 species. Species endemic to the Arctic Ocean comprise 51% whereas species endemic to the Arctic abyssal comprise 19%. Only two small genera are endemic to the Arctic Ocean. Genera with a worldwide distribution (60 genera or 65%) dominate the Arctic abyssal fauna. Most genera (55 or 60%) can be considered as deep-sea specialists, with half or more of the species in each genus occurring deeper than 2000 m. About one third of genera (37%) are known outside the Arctic in the hadal zone (>6000 m). The share of genera known from the hadal is probably higher in the Arctic abyssal than in the abyssal of other oceans. For many genera, the worldwide minimum or maximum of their depth ranges is found in the Arctic Ocean. Distribution patterns of genera suggest that many deep-sea Arctic species derive from their congeners distributed in geographically distant regions (primarily the Southern Ocean and the Indo-West Pacific). The deep-sea North Atlantic was the main transit region on the pathway to the Arctic. There is no firm evidence of the presence of derivatives of the pre-Pliocene deep-sea Arctic fauna in the modern Arctic fauna. Twelve genera (13%) with a worldwide distribution are recognized as the most reliable examples of the emergence of the abyssal fauna in the Arctic Ocean. Two genera (2%) are characterized by the following distribution and ecological patterns: (1) distribution is limited to the Northern Hemisphere, (2) wide bathymetrical range (from shelf to abyssal), (3) abyssal records only within the Arctic Ocean, and (4) very wide ranges of habitats. Arctic submergence of the shelf fauna to the abyssal zone is suggested for these genera. Some higher taxa, not considered in the present work in detail, may have a high share of genera with similar distribution patterns. For instance the share of genera having submerged from the Arctic shelf to the abyssal is about 25% in the abyssal Arctic amphipod fauna.

KEY WORDS: distribution patterns, genera, Arctic Ocean, abyssal, faunal submergence, faunal emergence.

Особенности глобального распространения родов, обитающих в Северном Ледовитом океане на глубинах более 2000 м

А.Н. Миронов, А.Б. Дильман, Е.М. Крылова

Институт океанологии им. П.П. Шишова РАН, Нахимовский проспект 36, Москва, 117997, Россия; e-mail: miron@ocean.ru

РЕЗЮМЕ: Список родов, представленных в абиссали (>2000 м) Северного Ледовитого океана составлен для 8 классов (Scaphopoda, Bivalvia, Crinoidea, Echinoidea, Holothuroidea, Asteroidea, Ophiuroidea и Ascidiacea) и некоторых отрядов, принадлежащих к классам Anthozoa, Maxillopoda и Malacostraca. Этот список включает 92 рода и 133 вида. Эндемичные для Северного Ледовитого океана виды составляют 51%, в то время как виды, эндемичные для арктической абиссали, составляют 19%. Только два мелких рода являются эндемиками Северного Ледовитого океана. В арктической абиссальной фауне доминируют роды, широко распространенные в Мировом океане (60 родов или 65%). Большинство родов (55 или 60%) можно также охарактеризовать как преимущественно глубоководные, то есть половина или более половины видов в каждом роду известны на глубинах более 2000 м. Приблизительно треть родов (37%) известна за пределами Арктического океана в хадальной зоне (>6000 м). Доля родов, известных из хадали, вероятно более высокая в арктической абиссали, чем в абиссали других океанов. Для многих родов самое мелководное или самое глубоководное нахождения сделаны в Северном Ледовитом океане. Особенности распространения родов показывают, что многие глубоководные арктические виды произошли от видов, обитавших в географически отдаленных районах (в первую очередь, в Южном океане и Индо-Вест Пасифике). Глубоководная северная Атлантика сыграла роль основного транзитного региона. Отсутствуют надежные свидетельства о существовании в современном Северном Ледовитом океане видов, произошедших от доплиоценовых глубоководных арктических предков. 12 родов (13%), широко распространенных в Мировом океане, рассматриваются как наиболее вероятные примеры поднятия абиссальной фауны в Северном Ледовитом океане. Распространение двух родов (2%) характеризуется одновременно следующими чертами: (1) распространение ограничено северным полушарием, (2) широкий диапазон вертикального распространения, (3) абиссальные нахождения только в Северном Ледовитом океане и (4) чрезвычайно широкий спектр биотопов. Для этих родов предполагается погружение фауны из арктического шельфа до абиссальной зоны. Роды с такими же особенностями распространения могут составлять большую долю в некоторых макротаксонах, детально не рассматриваемых в настоящей работе. Например, доля родов, погружившихся из арктического шельфа до абиссали, приблизительно равна 25% в абиссальной арктической фауне амфипод.

КЛЮЧЕВЫЕ СЛОВА: распространение, роды, Северный Ледовитый океан, абиссаль, погружение фауны, поднятие фауны.

1. Introduction

Different scenarios have been suggested for the origin of species prevailing in the Arctic abyssal fauna. Some authors suppose that the bulk of the Arctic abyssal fauna consists of immigrants from the Atlantic deep sea (Ekman, 1953; Filatova, 1962; Kussakin, 1979; Svavarsson et al., 1993; Smirnov, 1994; Sirenko et al., 2004; Bluhm et al., 2011; Krylova et al., 2013, and others). Others support the hypothesis of

the origin of the Arctic abyssal fauna mainly from the Arctic shelf fauna. Gurjanova (1938, 1951, 1970, 1985a) was the most consistent in developing the latter hypothesis. According to Gurjanova (1951), colonization of the Arctic depths by shallow-water species resulted in speciation in the abyssal zone, primarily in the Greenland Basin and adjacent areas of the Central Arctic. Gurjanova suggested that this deep-sea center of speciation occurred at the border between the Pliocene and the Pleistocene. She

explained some similarity between deep-sea faunas of the Arctic Ocean and the North Atlantic by two reasons. First, few deep-sea North Atlantic taxa penetrated the Norwegian and Greenland Seas. As a rule these taxa did not disperse further to the north and north-east. Second, this similarity results from penetration of some deep-sea species of the Arctic origin into the North Atlantic. Koltun (1964) also mentioned the possibility of dispersal of deep-sea species from the Arctic to the northern Atlantic. Gurjanova (1985a) as well as Derjugin (1915), Andriashev (1985), Golikov and Scarlato (1989) and others used the term "pseudoabyssal" to emphasize the lack of connection between the Arctic abyssal fauna and the true abyssal fauna of the World Ocean. It was repeatedly suggested that part of the shallow-water Arctic fauna has survived during the glaciation owing to migration to the depths of the Arctic Ocean (Gurjanova, 1939, 1957; Koltun, 1964; Nesis, 1983, 2001; Golikov, Scarlato, 1989; Svavarsson et al., 1993; Clarke, 2003).

To justify the hypothesis of the shelf origin Gurjanova mainly used data on distribution and relationships of amphipod genera and species. Just (1980b) emphasized the difference between abyssal faunas of amphipods and isopods: the Arctic abyssal amphipods belong mainly to genera occurring on adjacent shelves, whereas the majority of the asellote isopods belong to widespread deep-sea genera. Dahl (1979) mentioned a similar difference between the amphipod and molluscan faunas. According to Dahl, the Recent amphipod deep-sea fauna of the Norwegian Sea has the closest connection at the species and generic levels with the Arctic and high-boreal shelf fauna, whereas the deep-sea molluscan fauna seems to have no close affinity to the shelf fauna. A close relation is also suggested for shelf and abyssal fish fauna of the Arctic Ocean. As indicated by Haedrich and Krefft (1978), abyssal fish fauna of the Arctic Ocean consists of secondary deep-sea invaders from shallower depths. Andriashev (1985) believed that the true abyssal fish fauna of the World Ocean did not penetrate into the Arctic.

Most authors agree that colonization of the Arctic abyssal occurred relatively recently, in the Pleistocene. There is also a hypothesis about the pre-Pleistocene or even pre-Pliocene age of the Arctic abyssal fauna. Gorbunov (1946) suggested that some genera have no relatives on Arctic or boreal shelves and their abyssal species appeared before the first Quaternary glaciation. Menzies et al. (1973) believed that some endemic abyssal genera result from a step-wise evolution from shelf genera and species in the Pleistocene, whereas other genera that are evidently allied to abyssal genera in other oceans, submerged prior to the Pleistocene and their species and subspecies have evolved since then at abyssal depths. Bouchet and Warén (1979) presented a survey of the Arctic abyssal shell-bearing molluscs: altogether 31 species of 28 genera have been recorded at depths below 2500 m. The authors suggested that 10 species could be regarded as late Atlantic immigrants whereas 10 other species were more closely related to the abyssal Pacific fauna than to the Atlantic one. For the remaining 11 species the authors did not recognize any relatives. Bouchet and Warén (1979) gave the following explanation of the relationship to the North Pacific fauna: part of the deep sea Arctic fauna is a reminiscence of the old North Pacific fauna that lived in the Polar Basin before it was disconnected from the North Pacific by the Bering Strait. These species subsequently diverged only very slightly. Jirkov (2001) stated that the deep-sea Arctic fauna is older than the Arctic shallow-water fauna. Sirenko et al. (2004) suggest that the high number of endemics in the Arctic bathyal and abyssal indicated a rather long period of evolution of the deep-sea Arctic fauna. At the same time the authors noted significant influence of the shelf fauna on the bathyal and even abyssal faunas of the Arctic Ocean.

Only three pathways of colonization of the Arctic abyssal can be suggested: via the deep-sea North Atlantic (1), via the deep-sea North Pacific (2) and from the Arctic shelf-bathyal zone (3). However, the discussion about the biogeographical history of the Arctic abyssal fauna is considerably complicated by the fact

that faunas of all these three regions are of a multiple origin (see section 7). Possible scenarios get even more complicated if one takes into account that one and the same species could penetrate the Arctic abyssal repeatedly and by different pathways.

The present work describes global distribution patterns of genera represented in the abyssal of the Arctic Ocean. Our main goal was to reveal the types of distribution of the groups of genera that have been most successful in the colonization of the Arctic abyssal. Based on the distribution patterns of the most successful groups of genera, we hypothesize the main donor regions for the abyssal Arctic fauna.

2. Compilation of the genera list

The Arctic Ocean is considered here within borders adopted in the “Atlas of the Arctic” (Leontjev, 1985; Treshnikov, 1985). The Norwegian, Greenland and Chukchi Seas are included in the Arctic Ocean. The 2000 m horizon was arbitrarily taken as the upper boundary of the abyssal zone. Species are designated as “Arctic” if they occur in the Arctic Ocean. Species are designated as abyssal if they are recorded in the abyssal. For purposes of the current paper, these terms are used in a wide context: Arctic species are not only the Arctic endemics, but also the Arctic-Pacific, Arctic-Atlantic and cosmopolitan species; abyssal species are not only the abyssal endemics, but also bathyal-abyssal and sublittoral-abyssal species. Genera are designated as “abyssal” if they contain at least one abyssal species. (For different interpretations the notion ‘Arctic species’ see Jirkov, 2013; Mironov, 2013).

A complete list of genera recorded in the Arctic at depths exceeding 2000 m was compiled for eight classes (Scaphopoda, Bivalvia, Crinoidea, Echinoidea, Holothuroidea, Asteroidea, Ophiuroidea and Ascidiacea) and some orders from the classes Anthozoa, Maxillopoda and Malacostraca (Table 2). The abyssal Arctic fauna of these groups is the most studied. The list includes 92 genera (Table 1) and 133 species. Genera of Bivalvia known in the Arctic

only by empty shells from deeper than 2000 m were not listed. Thus, Richling (2000) reported empty shells of the following genera deeper than 2000 m north of the Laptev Sea: *Arctinula*, *Astarte*, *Cardiomya*, *Ciliatocardium*, *Cyrtodaria*, *Hiatella*, *Liocyma*, *Lyonsia*, *Macoma*, *Nuculana*, *Serripes*, *Similipekten* and *Yoldia*. The genus *Portlandia* was included in the list of abyssal genera tentatively since data on its vertical distribution are inconsistent. Filatova (1951) mentioned live individuals of *Portlandia arctica* from 10–350 m depth, with empty shells occurring deeper than 2000 m. In her opinion, the valves could be transported to the abyssal by currents and ice. Coan et al. (2000) believe that live *P. arctica* occur only to 500 m. However, live specimens were reported by Bernard (1979) from 2560 m in the Beaufort Sea.

A list of selected genera occurring deeper than 2000 m was compiled for the Arctic Amphipoda. Genera in this list are those with a close relationship between the Arctic abyssal and shelf species. The list includes 16 genera out of 64 abyssal (Table 2). For each genus Tables 1 and 2 show the vertical distribution ranges of species recorded in the Arctic Ocean and species unknown in the Arctic Ocean. Depth ranges of the Arctic species are given for the World Ocean (not only for the Arctic basin).

Our list of genera is based on published sources. The main publications used are listed in Table 3. Three echinoderm genera were included in the list, based on unpublished data. One specimen of *Myriotrochus* (Holothuroidea) was found in the Canada Basin at depth of approximately 2500 m (RV *Healy*, 2005, leg. 02, Sta. 15, identified by A.N. Mironov). The genera *Gracilechinus* (Echinoidea) and *Ceramaster* (Asteroidea) were recorded in the Norwegian Basin at depth 2198 m (RV *Sevastopol*, cruise 8, Sta. 1351, 25.03.58, 69°39'N, 15°01'W, identified by K.V. Minin and A.B. Dilman correspondingly).

Data on the total number of species in a genus were taken mainly from the World Register of Marine Species (WoRMS) (Appeltans et al., 2012). However, there were several exceptions. To six species indicated for the bivalve

Table 1. Distribution of genera known from the Arctic Ocean at deeper than 2000 m. NA — N Atlantic, SA — S Atlantic, NP — N Pacific, SP — S Pacific, IO — Indian Ocean, SO — South Ocean, COS — cosmopolitan distribution. The boundary line between the North and South Atlantic and Pacific Oceans is the Equator.

Таблица 1. Распространение родов, известных в Северном Ледовитом океане на глубинах более 2000 м. NA — Сев. Атлантика, SA — Южная Атлантика, NP — Сев. Пацифика, Южная Пацифика, IO — Индийский океан, SO — Южный Океан, COS — космополитное распространение. Экватор принят за пограничную линию между северными и южными половинами Атлантического и Тихого океанов.

Genera	Number of species in the genus (in the Arctic Ocean*)	Distribution of species unknown in the Arctic Ocean	Depth range, m	
			Species known from the Arctic Ocean**	Species unknown in the Arctic Ocean
Class ANTHOZOA				
Subclass Hexacorallia				
<i>Amphianthus</i>	27 (4/1)	NA, SA, NP, SP, IO	130–3870	0–5300
<i>Anthosactis</i>	7 (2/1)	COS	11–3337	280–4100
<i>Antipodactis</i>	2 (1/1)	SO	2377	2852–3239
<i>Bathypheilia</i>	2 (1/1)	NP, SO	400–5569	3200–4575
<i>Cerianthus</i>	28 (4/1)	NA, SA, NP, SP, IO	0–2878	0–5248
<i>Epizoanthus</i>	85 (?/1)	NA, SA, NP, SP, IO	73–2104	5–4667
<i>Kadosactis</i>	5 (2/1)	NA, SO	475–2576	70–4710
<i>Oceanactis</i>	3 (1/1)	NP, SP	3012–3028	558–1280
<i>Sagartiogeton</i>	12 (1-2/1)	NA, NP, SP	240–2410	0–2145
Class MAXILLOPODA				
Order Scalpelliformes				
<i>Verum</i>	23 (1/1)	NA, SA, NP, SP, IO	348–3941	204–4850
Class MALACOSTRACA				
Order Isopoda				
<i>Austroniscus</i>	10 (1/1)	NA, SA, NP, SO	2470–3642	10–6850
<i>Balbidocolon</i>	2 (1/1)	NA, SA, ?SP	3350	1648–5389
<i>Caecognathia</i>	46 (4/2)	COS	0–3000	0–2638
<i>Cryodesma</i>	2 (2/2)	Endemic to the Arctic Ocean	417–3672	–
<i>Desmosoma</i>	32 (4/1)	COS	17–2887	20–6134
<i>Disconectes</i>	13 (3/2)	COS	54–3410	15–7934
<i>Eurgerda</i>	17 (8/3)	NA, NP	4–3003	30–4825
<i>Eugerdella</i>	19 (2/1)	NA, SA, NP, SO	16–3620	24–6000
<i>Eurycope</i>	57 (10/9)	COS	46–3970	213–9174
<i>Exilinisus</i>	4 (1/1)	NA, SA, NP	80–3920	1964–5023
<i>Gracilimesus</i>	12 (4/1)	NA, SA, NP, SP	698–5494	1491–4925
<i>Gurjanopsis</i>	2 (1/1)	SO	1279–3709	3405–4655
<i>Haplomesus</i>	5 (1/1)	NA, SA, NP, SO	365–4150	2641–6135
<i>Haploniscus</i>	73 (2/2)	COS	698–5024	385–8345
<i>Heteromesus</i>	18 (1/1)	NA, SA, NP	539–2104	364–8330
<i>Ilyarachna</i>	41+?12 (7/5)	COS	8–5223	50–7230 (?10687)

Table 1 (continuing)
Таблица 1 (продолжение)

<i>Ischnomesus</i>	39 (4/1)	COS	94–2681	274–8330
<i>Macrostylis</i>	80 (5/2)	COS	4–3510	149–10730
<i>Mirabilicoxa</i>	19 (1)	NA, NP, SP	2194–3806	530–6710
<i>Munna</i>	80 (11/1)	COS	0–3709	0–3839
<i>Munneurycope</i>	12 (1)	COS	2370–2750	400–8400
<i>Nannoniscus</i>	31 (10/4)	COS	40–5843	4–6328
<i>Oecidiobranthus</i>	5 (4/1)	NA, SP	40–3920	2055
<i>Panetela</i>	3 (1/1)	SA, NP	3230	1427–5495
<i>Paramunnopsis</i>	4 (1/1)	COS	2675–3970	0–3240
<i>Pseudomesus</i>	5 (1/1)	NA, SA, NP, SP	80–3709	1119–5441
<i>Rapaniscus</i>	3 (1/1)	NA, SA	219–2754	1254–5389
<i>Saduria</i>	4 (4/3)	-	0–3127	-
<i>Whoia</i>	4 (1/1)	NA, SP	1279–2024	50–4892
Order Mysida				
<i>Amblyops</i>	12 + ?10 (1/1)	COS	49–2681	170–7230
<i>Amblyopsoides</i>	4 (1/1)	COS	1940–2681	503–2928
<i>Birsteiniamysis</i>	2 (1/1)	NP	750–7200 (COS)	(abyssal)
<i>Dactylamblyops</i>	15 (1/1)	NA, NP, SP, IO, SO	49–4320	0?–350–4500
<i>Michthyops</i>	3 (2/2)	NA	27–3550	200–2630
<i>Pseudomma</i>	44 (4/1)	COS	12–2340	18–3425
<i>Pseudomysis</i>	2 (1/1)	NP	1421–3081	500–1200
Order Euphausiacea				
<i>Thysanoessa</i>	10 (4/3)	COS	0–3320	0–3000
Order Decapoda				
<i>Bythocaris</i>	17 (10/5)	NA	50–3800	74–2120
<i>Hymenodora</i> (pelagic)	4 (1/1)	COS	100–5440 (COS)	0–5300
<i>Pasiphaea</i>	71 (3/1)	COS	10–3219– ?5551	0–2853
Class SCAPHOPODA				
<i>Siphonodentalium</i>	18 (2/2)	COS	16–3254	36–4734
Class BIVALVIA				
<i>Axinulus</i>	8 (3/1)	COS	20–4632	42–7434 (10015)
<i>Bathyarca</i>	27 (3/1)	COS	6–4170	0–5175
<i>Cuspidaria</i>	120 (8/3)	COS	0–4453	0–7335
<i>Dacrydium</i>	29 (2/1)	COS	5–4060	45–6150
<i>Ennucula</i>	47 (3/1)	COS	20–2250	50–3910
<i>Hyalopecten</i>	10 (1/1)	COS	1060–3920	400–7000
<i>Katadesmia</i>	7 (1/1)	COS	1036–3965	523–7320
<i>Kelliola</i>	1 (1/1)	-	?892–2006– 4150	-
<i>Mendicula</i>	7 (4/3)	NA, SA, NP, SP, IO	8–4825	27–5223
<i>Myonera</i>	19 (1/1)	COS	2300–3709	400–8035
<i>Nucula</i>	96 (6/1)	COS	5–2589	5–4938
<i>Policordia</i>	25 (2/1)	COS	1223–3700	73–9380

Table 1 (continuing)
Таблица 1 (продолжение)

<i>?Portlandia</i>	6 (3/?1)	NA, SO	2–350–?2560	27–1334
<i>Tindaria</i>	28 (1/1)	COS	1125–3800	60–6210 (7286)
<i>Yoldiella</i>	98 (13/5)	COS	7–3800	20–7333
Class CRINOIDEA				
<i>Bathycrinus</i>	10 (1/1)	COS	460–3800	693–9345
<i>Conocrinus</i>	?6 (1/1)	NA, NP, SP	140–3135	290–2070
Class ECHINOIDEA				
<i>Gracilechinus</i>	8 (3/1)	NA, SA, NP, SP	20–4700	120–2700
<i>Pourtalesia</i>	12 (1/1)	COS	220–3081	227–7340
Class HOLOTHUROIDEA				
<i>Acanthotrochus</i>	3 (1/1)	NP, SO	1015–3900	2800–4730
<i>Elpidia</i>	22 (3/2)	COS	70–5550	650–9700
<i>Kolga</i>	3 (1/1)	NA, SO, NP	659–4106	1484–6235
<i>Molpadia</i>	56 (2/1)	COS	40–2785	4–5870
<i>Myriotrochus</i>	16 (3/1)	COS	2–2500	2–9174
<i>Prototrochus</i>	19 (2/1)	COS	600–3900	60–10687
Class ASTEROIDEA				
<i>Bathybiaster</i>	2 (1/1)	NA, SA	160–3110	80–880
<i>Ceramaster</i>	17 (1/1)	NA, SA, NP, SP, IO	40–2198	0–2500
<i>Henricia</i>	79 (9/1)	COS	0–4204	0–1635
<i>Hymenaster</i>	49 (1/1)	COS	15–3527	405–9990
<i>Pontaster</i>	1 (1/1)	–	16–3440	–
<i>Poraniomorpha</i>	5 (4/2)	NA	9–3072	2995–3740
<i>Tylaster</i>	1 (1/1)	Endemic to the Arctic Ocean	79–2920	–
Class OPHIUROIDEA				
<i>Ophiacantha</i>	128 (4/1)	COS	7–4730	0–6235
<i>Ophiocten</i>	21 (2/1)	COS	5–4500	8–6070
<i>Ophiopleura</i>	2 (1/1)	NA	10–2500	150–1875
<i>Ophioscolex</i>	8 (1/1)	NA, SA, NP, SP, IO	35–2727	99–1246
<i>Ophiostriatus</i>	4 (1/1)	NA, SA, NP, IO, SO	270–4000	40–6150
Class ASCIDIACEA				
<i>Araneum</i>	2 (1/1)	SP	1386–5223	570–610
<i>Asajirus</i>	6 (1/1)	NA, SA, SP, IO	850–7420 (COS)	600–4829
<i>Dendrodoa</i>	6 (5/1)	NP	0–2340	0–12
<i>Styela</i>	82 (6/1)	COS	0–2195	0–6330
Total: 92 genera				

* In brackets: numbers of species known from the Arctic Ocean and from the Arctic abyssal zone (>2000 m).

** Including occurrences outside the Arctic Ocean

* В скобках: число видов, встречающихся в Северном Ледовитом океане и в Арктической абиссальной зоне (>2000 м).

** включая находения за пределами Северного Ледовитого океана.

Table 2. Distribution of the amphipod genera in the abyssal fauna with a presumed Arctic shelf origin. Abbreviations as in Table 1.

Таблица 2. Распространение родов амфипод в абиссальной фауне, для которой предполагается происхождение от фауны Арктического шельфа. Сокращения как для таблицы 1.

Genera	Number of species in the genus (in the Arctic Ocean)	Distribution of species unknown in the Arctic Ocean	Depth range, m	
			Species known from the Arctic Ocean	Species unknown in the Arctic Ocean
<i>Aeginina</i>	2 (2/1)	–	5–2258	–
<i>Ambasia</i>	1 (1/1)	–	75–1096 (?2681)	–
<i>Apherusa</i>	20 (10/1)	NA, NP	0–2681	0–126
<i>Arrhis</i>	4 (2/1)	NA, NP	10–3268	100–105
<i>Boeckosimus</i>	13 (13/1)	–	5–3200	–
<i>Cleippides</i>	3 (2/1)	NA	28–2990	1380–1900
<i>Deflexilodes</i>	15 (8/1)	NA, NP	5–2222	0–200
<i>Halirages</i>	8 (8/4)	–	0–5375	–
<i>Haliragoides</i>	4 (3/1)	SO	30–2500	16–18
<i>Ischyrocerus</i>	42 (17/3)	COS	0–2681	0–2454
<i>Metacaprella</i>	4 (1/1)	NP	35–2365	0–104
<i>Neohela</i>	5 (3/1)	NP	47–2806	140–200
<i>Onisimus</i>	13 (11/1)	Caspian Sea	0–3300	100–457
<i>Paroediceros</i>	5 (4/1)	NA	5–2681	11–80
<i>Paronesimus</i>	1 (1/1)	–	24–2450	–
<i>Tmetonyx</i>	13 (8/2)	NA, SO	8–3800	0–160

genus *Axinulus* in WoRMS, we added *A. careyi* Bernard 1979 and *A. hadalis* (Okutani, Fujikura, Kojima, 1999). Seven species listed in WoRMS for the bivalve genus *Mendicula* were supplemented by two abyssal species, which were earlier considered as representatives of the genus *Thyasira*: *Thyasira* (*Mendicula*) *ockelmanni* Keuning & Schander, 2010 (?= *Thyasira* sp.n. Bouchet & Warén, 1979) and *T. otoschmidti* Gorbunov, 1946. Therefore the genus *Thyasira* was not included in the list of Arctic abyssal genera. Following Bouchet and Warén (1979) and Knudsen (1985), we regard the bivalve *Malletia abyssopolaris* Clarke as a junior synonym of *Tindaria derjugini*. The number of species in the bivalve genus *Portlandia* was reduced from eight to six: *P. glacialis* was accepted as *P. arctica* and *P. intermedia* as *Yoldiella intermedia*. The composition of the holothurian genus *Elpidia* follows that of Gebbruk and Rogacheva (2010) (see also Budaeva, Rogacheva, 2013). The composition of the genus *Gracilechinus* (Echinoidea) was modified

after Minin et al. (2012; Minin, in preparation) who showed, based on molecular data, that the following 10 species should be assigned to this genus: *G. acutus*, *G. affinis*, *G. alexandri*, *G. atlanticus*, *G. elegans*, *G. euryporus*, *G. gracilis*, *G. lucidus*, *G. multidentatus* and *G. stenoporus*. WoRMS lists eight species each for the ascidian genera *Asajirus* Kott and *Dendrodoa* MacLeay. We did not accept all of them, after consultations with the expert Karen Sanamyan (6 species in Table 2). In particular, *Asajirus arcticus* was accepted as *A. indicus* with a cosmopolitan distribution.

Data on geographical and vertical distribution of 92 genera in the World Ocean were taken from several hundred publications. To characterize schematically the distribution of genera in the World Ocean, we divided it into seven large regions: the Arctic Ocean, North Atlantic (NA), South Atlantic (SA), North Pacific (NP), South Pacific (SP), the Southern Ocean (SO) and the Indian Ocean (IO). The boundary line between the North and South regions in the Atlantic and

Table 3. Main publications used to compile the list of the Arctic abyssal genera (>2000 m).
 Таблица 3. Основные публикации, использованные для составления списка Арктических абиссальных родов (>2000 м).

Class	Main publications
Anthozoa (Hexacorallia)	Danielsen, 1890; Carlgren, 1913, 1942; Jensen, 1992; Fautin, 2006
Maxilopoda (Scalpelliformes)	Sars, 1886; Broch, 1953; Tarasov, Zevina, 1957
Malacostraca (Decapoda, Euphausiacea, Isopoda, Mysida, Amphipoda)	Sars, 1886; Hansen, 1916; Stephensen, 1923, 1925, 1931, 1944; Gurjanova, 1946, 1951, 1964; Barnard et al., 1962; Bulycheva, 1964; Lomakina, 1964; Dahl, 1979; Kussakin, 1979, 1982, 1988, 1999, 2003; Just, 1980a, b; Petrashov, 1993, 2004; Svavarsson et al., 1993; Malyutina, Kussakin, 1996a, b, c; Brandt, 1997, 2005; Sokolov, 2000; Kamenskaya, 2001; Malyutina, Weissappel, 2001; Vader et al., 2005; Brix, Svavarsson, 2010
Scaphopoda	Bouchet, Warén, 1979; Ivanov, Zarubina, 2004
Bivalvia	Bernard, 1979; Bouchet, Warén, 1979; Knudsen, 1985; Richling, 2000
Crinoidea	Clark, 1970, Rogacheva et al., 2013
Echinoidea	Mortensen, 1903, 1907; Mironov, 1995;
Holothurioidea	Madsen, Hansen, 1994; Rogacheva, 2007; Rogacheva et al., 2013
Asteroidea	Danielssen, Koren, 1884; Clark, 1989, 1993, 1996; Clark, Mah, 2001
Ophiuroidea	Mortensen, 1933; Djakonov, 1954; Stöhr, O'Hara, 2012
Ascidiacea	Hartmeyer, 1923; Millar, 1966; Monniot, Monniot, 1979
Several classes	Gorbunov, 1946; Baranova, 1964; Koltun, 1964; Afanasjev, Filatova, 1980; Smirnov, 1994; Kröncke, 1998; Deubel, 2000; Sirenko, 2001; Sirenko et al., 2004; Smirnov, Smirnov, 2006; Budaeva et al., 2008; Bergman et al., 2009; Soltwedel et al 2009; MacDonald et al., 2010; Appeltans et al., 2012

the Pacific Oceans is the equator. The zone of the Antarctic Convergence was taken as the northern boundary of the Southern Ocean. This zone is varying in latitude at different longitudes, extending across the Atlantic, Pacific and Indian Oceans between 48 and 61°S. The Falkland Islands, Prince Edward Islands, Crozet Islands, Île Amsterdam, Île Saint-Paul, Tierra del Fuego and Macquarie Island lie north of the Antarctic Convergence. The Kerguelen Islands lie approximately on the Convergence. The South Shetland Islands, South Orkney Islands, South Georgia and the South Sandwich Islands, Bouvet Island, Heard Island and McDonald Islands all occur south of the Convergence. The macrotaxa we used include representatives of different ecological groups: benthic and pelagic forms, infaunal and epibenthic animals, errant and sedentary, filter-feeders, predators and detritophages, parasites and commensals. The diversity of macrotaxa and the number of abyssal genera used in the present work should be sufficient enough to reveal general distribution patterns

characteristic of the Arctic abyssal macro- and megafauna. Meiobenthic taxa were excluded from our analysis.

3. Species distribution patterns

It was repeatedly mentioned in publications that the Arctic Ocean fauna is characterized by a high degree of endemism at the species level (Gurjanova, 1938, 1951, 1970; Gorbunov, 1946; Ekman, 1953; Menzies, 1963; Dahl, 1972, 1979; Menzies et al., 1973; Bouchet, Warén, 1979; Kussakin, 1979; Just, 1980b; Svavarsson et al., 1993, Vinogradova, 1997 and others). Our calculations confirm this conclusion. Species endemic to the Arctic Ocean comprise more than half of the Arctic abyssal faunal species (68 species, or 51%) (Table 4). At the same time, the bulk of the Arctic abyssal fauna consists of eurybathic species with an upper distribution limit on the shelf or slope (Table 4). Among Arctic endemics occurring in the abyssal, only 25 species are endemics of the abyssal zone

Table 4. Distribution patterns of Arctic abyssal species and genera.
Таблица 4. Особенности распространения Арктических абиссальных видов и родов.

Distribution pattern	Number of taxa	
	species	genera
The Arctic Ocean, >2000 m	133 (100%)	92 (100%)
I. Within the Arctic Ocean		
Norwegian and Greenland Seas	110 (83%)	87 (94.5%)
Norwegian and Greenland Seas only	19 (14%)	11 (12%)
High-Arctic Basin	113 (85%)	81 (88%)
High-Arctic Basin only	22 (16.5%)	5 (5.5%)
Endemics to the Arctic Ocean	68 (51%)	2 (2%)
II. Outside the Arctic Ocean		
Common with N Atlantic	62 (47%)	81 (88%)
N Atlantic and Arctic only	42 (31.5%)	5 (5.5%)
Common with S Atlantic	10 (7.5%)	63 (68%)
Common with N Pacific	18 (13.5%)	73 (79%)
Common with S Ocean	4 (3%)	53 (58%)
Common with north hemisphere	63 (47%)	87 (94.5%)
Common with south hemisphere	10 (7.5%)	79 (86%)
World-wide distribution (4 and more regions, without the Arctic Ocean)	3 (2%)	60 (65%)
III. Most shallow depth of occurrence		
Deeper than 2000 m	27 (20%)	2 (2%)
Between 1001 and 2000 m	16 (12%)	4 (4%)
Between 201 and 1000 m	36 (27%)	22 (24%)
Between 0–200 m	54 (41%)	64 (70%)
IV. Known in the hadal zone (deeper than 6000 m)	2 (1.5%)	34 (37%)
V. Genera in which $\geq 50\%$ of species were recorded from depths exceeding 2000 m	–	55 (60%)

whereas 43 species occur both shallower and deeper than 2000 m. Hence, endemics of the abyssal zone in the Arctic Ocean comprise 19% of the Arctic abyssal species fauna. Abyssal zone endemics are usually known only from a few records. For example, the following species are considered as endemics based on single record: the actinarians *Antipodactis awii* and *Oceanactis bursifera*, the isopods *Balbidocolon polare*, *Cryodesma cryoabyssale*, *Eurycope septentrionalis*, *Eurycope vasinae* and *Panetela compacta* and the ascidian *Styela bathybia*. Further studies will probably show that these species also occur shallower than 2000 m, and that the share of the abyssal zone endemic species in the Arctic is much less than 19%.

The abyssal fauna is rather homogeneous over the entire Arctic Ocean. The most marked difference is between the Norwegian/Green-

land Seas and the high-Arctic Basin faunas: 92 species (69%) occur both in the Norwegian/Greenland Seas and the high-Arctic Basin, 19 species are distributed only in the Norwegian and Greenland Seas and 22 species occur only in the high-Arctic Basin. Pan-Arctic distribution is characteristic of many eurybathic endemics of the Arctic Ocean. These endemics are abundant and they define features of benthic communities over vast areas of the seafloor. For example, pan-Arctic endemic echinoderms *Bathycrinus carpenteri*, *Pourtalesia jeffreysi*, *Ophiopleura borealis*, *Elpidia belyaevi*, *E. heckeri* and *Kolga hyalina* often dominate in the abyssal benthic communities.

Almost all Arctic abyssal species known outside the Arctic Ocean (62 out of 65) are common with the North Atlantic. Species common with other regions of the World Ocean are

few (Table 4). This peculiarity suggests the distribution pathway of the Arctic deep-sea fauna via the North Atlantic.

Species with a bipolar distribution are not known. Species with a cosmopolitan distribution are very few: the benthopelagic shrimp *Hymenodora glacialis* (100–5440 m), the benthopelagic mysid *Birsteiniamysis inermis* (750–7200 m) and the benthic ascidian *Asajirus indicus* (850–7420 m). In some genera there are pairs of species with one being endemic of the Arctic Ocean and the other being widely distributed in the World Ocean except for the Arctic. For example, the Arctic endemic *Paramunnopsis justii* (2675–3970 m) and the widely distributed *P. oceanica* (0–2300 m), *Munneurycope glacialis* (2370–2750 m) and *M. murrayi* (400–7800 m).

Rare examples of deep-sea cosmopolites in other benthic taxa are the brachiopod *Pelagodiscus atlanticus* (366–5530 m, empty shells down to 7600 m) (Zezina, 1980), the sipunculids *Golfingia vulgaris* (0–5853 m), *Nephasoma minutum* (0–6170 m) and *Phascolion strombus* (1–4030 m) (Murina, 1961; Murina, Sørensen, 2004), the amphipods *Eurythenes gryllus* (550–7800 m) (Brandt et al., 2012) and *Scina borealis* (50–3000 m) (Bulicheva, 1964; Vinogradov et al., 1996) and the polychaetes *Amphicteis gunneri* (12–7686 m) and *Notomastus latericeus* (0–6230 m). Cosmopolitan species in general are rather rare in the abyssal mega- and macrofauna of the Arctic Ocean. They are more characteristic for meiofauna and plankton. The share of species with a world-wide distribution probably reaches a maximum in the biota of planktonic protozoans. For instance, there are 34 species with the Arctic-boreal-tropical distribution, 9 bipolar species and 12 cosmopolitan among the Arctic planktonic dinoflagellates (Okolodkov, 1999). True Arctic species among planktonic dinoflagellates (Okolodkov, 1999) and planktonic diatoms (Beklemishev, Semina, 1986) are not known.

4. Distribution patterns of genera

Endemics of the Arctic Ocean, among the abyssal genera, comprise only 2%: the isopod

Cryodesma with two species and the asteroid *Tylaster* with a single species (Table 1). Both genera are eurybathic and widely distributed within the Arctic Ocean. The abyssal fauna of the Arctic Ocean almost entirely consists of eurybathic (bathyal-abyssal, sublittoral-abyssal, bathyal-hadal and sublittoral-hadal) genera (Tables 1 and 4). There are no genera endemic to the Arctic abyssal.

Most genera are represented in the Arctic Ocean by only a few species. In the majority of genera (73 out of 92, or 79%) there is only one Arctic abyssal species. In 44 of these, the abyssal species is the only Arctic species in the genus. The highest number of Arctic species (13, with 5 being abyssal) is found in the bivalve genus *Yoldiella*. The highest number of Arctic abyssal species (9) is recorded in the genus *Eurycope* (Table 1).

The generic composition of the abyssal fauna changes markedly at the transition from the Norwegian and Greenland Seas to the Arctic Basin: 11 genera (12%) are known only in the Norwegian and Greenland Seas, and five occur only in the Arctic Basin (Table 4).

Most Arctic genera (55 or 60%) can be characterized as “true” deep-sea genera, with half or more of species (per genus) recorded from depths exceeding 2000 m. Every third genus (37%) is known from the hadal zone (>6000 m) outside the Arctic Ocean (Tables 1 and 4). The share of genera known from the hadal is probably higher in the Arctic abyssal than in the abyssal of other oceans. For example, the share of hadal genera in echinoids is 50% in the Arctic abyssal and only 14% (6 out of 44 genera) in the abyssal zone outside the Arctic Ocean; the respective shares of hadal genera are 50% and 15% (3 out of 20 genera) in the stalked crinoids, and 60% and 23% (25 of 107 genera) in the bivalve abyssal fauna.

All abyssal Arctic genera can be divided into two groups, with regard to the extent of their distribution ranges in the World Ocean: genera with a world-wide distribution and genera with a limited distribution. Among the first, each genus is known outside the Arctic in four or more regions, whereas in the second group each

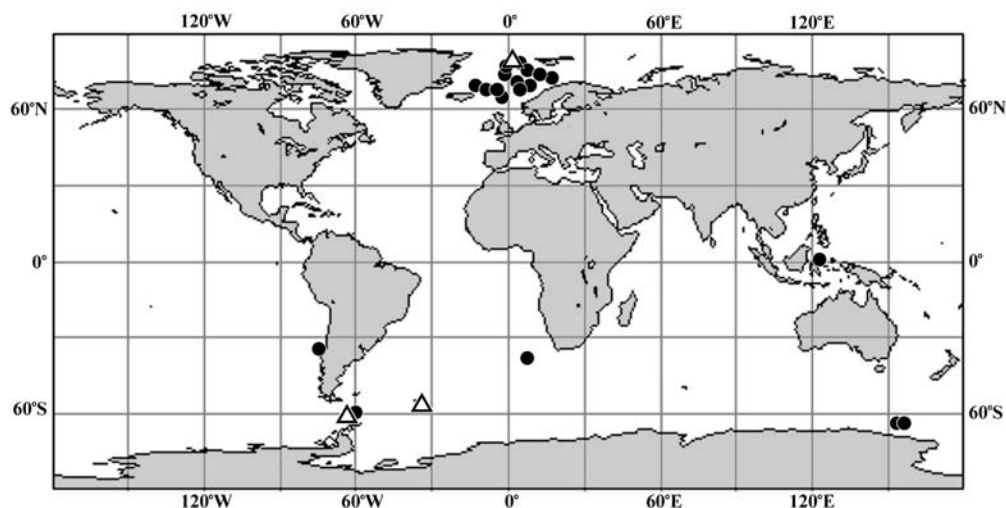


Fig. 1. Examples of genera with a disjunct distribution in the Atlantic Ocean. Distribution of sea anemones *Antipodactis*, at 2377–3239 m (triangles) and holothurians *Acanthotrochus*, at 1015–4730 m (circles). After Rodríguez et al. (2009), Belyaev and Mironov (1981), Madsen and Hansen (1994).

Рис. 1. Примеры родов с разрывом в распространении в Атлантическом океане. Распространение актиний *Antipodactis*, глубины 2377–3239 м (треугольники) и голотурий *Acanthotrochus* (кружочки), глубины 1015–4730 м. По Rodríguez et al. (2009), Беляеву и Миронову (1981), Madsen and Hansen (1994).

genus occurs in three or less regions. Genera with world-wide distribution dominate in the Arctic abyssal fauna: 60 or 65% (Table 4). These genera are usually species-rich, with four species and more. An exception is the isopod genus *Birsteiniamysis* with only two species, the cosmopolitan *B. inermis* and the North Pacific *B. caeca*.

Genera with a limited distribution (32 or 35%) generally contain fewer species: 21 genera with 1–4 species and 11 genera with more than 4 species. Among genera with limited distribution, the following are bipolar: *Antipodactis* (Fig. 1), *Bathypheilia*, *Kadosactis*, *Gurjanopsis* and *Kolga*. These genera occur in high northern and southern latitudes but are absent in low latitudes. The ranges of genera *Oceanactis*, *Whoia*, *Portlandia* and *Bathybiaster* are with wide disjunction in the equatorial zone (anti-tropical distribution). But they are either not known from the Southern Ocean or occur off Kerguelen (*Portlandia*), at the northern limit of the Southern Ocean. Thirteen genera are unknown from the Southern Hemisphere. At least

half of species in each of these genera occur in the Arctic (Table 1). Most genera in this group (9 out of 13) have their maximum depth of occurrence in the Arctic Ocean. Genera with a limited distribution generally show a higher linkage to the North Atlantic fauna than to the North Pacific: seven genera are common with the North Atlantic, two with the North Pacific, two both with the North Atlantic and the North Pacific and two are endemic to the Arctic Ocean. This pattern also supports the hypothesis about colonization of the Arctic abyssal mainly through the North Atlantic. Additional data on Arctic genera not found in the Southern Hemisphere are given below, in sections 5 and 8.

5. Deep-sea North Atlantic as a transit region

In theory there are three pathways of colonization of the Arctic abyssal (see Introduction): from the deep-sea North Atlantic, the deep-sea North Pacific and from the Arctic shelf-bathyal. The main pathway is from the deep North Atlan-

tic. Examples of colonization from the Arctic shelf are much fewer (see sections 7 and 8). Reliable examples of dispersal from the deep-sea North Pacific directly to the deep-sea Arctic are unknown.

The deep-sea fauna of the North Atlantic can be divided by origin into the following groups of species: (1) having dispersed without speciation from southern deep-sea regions, such as the Indo-West Pacific, Southern Ocean and South Atlantic, (2) species of the North Atlantic origin deriving from southern deep-sea species, (3) having dispersed without speciation from shallow waters of the North Atlantic; (4) species of the North Atlantic deep-sea origin deriving from shallow-water North Atlantic species, (5) species of deep-sea origin in the North Atlantic (speciation in the North Atlantic deep-sea), (6) having dispersed from the deep-sea Arctic Ocean (without speciation) and (7) having radiated from the Arctic deep-sea species. Each of these groups can be a potential donor of the Arctic abyssal fauna.

Two deep-sea families, the holothurians Elpidiidae and the echinoids Pourtalesiididae, give good examples of the transit role of the North Atlantic on the way to the Arctic. The biogeographical history of these families is connected with the deep-sea Antarctic centre of marine fauna redistribution (Belyaev, 1975; Mironov, 1980, 1982, 2006a, 2008; Gebruk, 1994; Rogacheva, 2007; see also below, section 7). The elpidiids *Elpidia* and *Kolga* are represented in the North Atlantic by *E. gracilis* and *K. nana* with a North Atlantic – Antarctic distribution. Both species belong to the first group by origin. The Arctic species of *Elpidia* and *Kolga* are endemic to the Arctic and they are more closely related to the North Atlantic-Antarctic species than to the North Pacific species (Rogacheva, 2007, 2011; Budaeva, Rogacheva, 2013). The North Atlantic species of *Pourtalesia* do not occur in the Antarctic or Indo-West Pacific, they belong to the second group of species. The Arctic endemic *P. jeffreysi* is closely related to *Pourtalesia* sp. from the Rockall Trough.

The example of species from the third group is the echinoid *Gracilechinus acutus*. It is known

from the west Barents Sea southward to the Angola coast and the Walvis Ridge at depths 20–2635 m. This species (and the genus as a whole) is known from the Arctic abyssal (2198 m) only from single occurrence in the Norwegian Sea. Both the genus and the species are of the North Atlantic shelf origin (Tyler, Young, 1998; Mironov, 2006; Minin, 2012; Rogacheva et al., 2013). Recent molecular studies support this scenario (Minin et al., 2012; Minin, pers. com.).

The sublittoral-abyssal genera *Michthyops*, *Bythocaris*, *Poraniomorpha* and *Ophiopleura* are known, besides in the Arctic, only in the North Atlantic. Thus, their North Atlantic species belong to one of the groups of the North Atlantic or Arctic origin (groups 3-7).

Some abyssal Arctic species lack close relatives in the North Atlantic. The corresponding genera dispersed via the North Atlantic without settling in this region. For example, the Arctic stalked crinoid *Bathycrinus carpenteri* is not closely related to the North Atlantic *B. gracilis*, but is similar to the *B. australis*. The latter occurs in the Antarctic, the Argentina Basin, the Angola Basin and north of the Kermadec Trench (Eléaume et al., 2012). The Arctic isopod *Balbidocolon polare* also differs considerably from the North Atlantic species *B. atlanticum* (Malyutina, Kussakin, 1996b).

The actinarian *Antipodactis* and the holothurian *Acanthotrochus* occur in the Arctic Ocean only in the Greenland/Norwegian Basin (Fig. 1). Both genera are not known from the North Atlantic. Outside the Arctic Ocean, *Antipodactis* was recorded only in the Southern Ocean (Rodríguez et al., 2009) and *Acanthotrochus* was found in the Southern Ocean and the Celebes Sea (Belyaev, Mironov, 1981). These two genera either did not settle in the North Atlantic dispersing through this region or became extinct there.

Genera with species from groups 1 and 2 (related to southern species) are much more numerous in the Arctic abyssal fauna than others. This suggests that the southern deep-sea regions (the Indo-West Pacific and the Southern Ocean) were the main donors of the Arctic abyssal fauna.

6. Probable pre-Pliocene deep-sea fauna of the Arctic Ocean

Data on macrofauna of the Arctic Ocean in the Paleogene and the Miocene are almost completely lacking. Among the Recent bivalve molluscs only *Cyrtodaria* was found in the Arctic pre-Pliocene deposits (Nesis, 1965; Strauch, 1972; Kafanov, 1979). This genus includes two Recent species, *C. kurriana* and *C. siliqua*, and 5 extinct ones. Today, *C. kurriana* is distributed throughout the Arctic (circumpolar) and in the North Pacific, whereas *C. siliqua* is known only from the North Atlantic. Live *Cyrtodaria* were found at 1–165 m depth, empty shells were recorded in the Arctic down to 3076–3081 m depth (Richling, 2000). There are also reports of *C. kurriana* from the Arctic bathyal and abyssal without indication of condition (live or dead) of the molluscs (Gorbunov, 1946; Rosenberg, 2009). Gorbunov (1946) reported *C. kurriana* from depths of 1475–1510 m and 1630–1900 m (Sadko Sts. 98 and 99). According to Rosenberg (2009) *C. kurriana* occurs at depths from 1 to 2362 m.

The distribution of *Cyrtodaria* has changed over geological time. Paleocene records are in the Arctic Ocean (Svalbard) and England, Middle-Upper Oligocene — in Europe, the northern Ustyurt (between the Caspian and Aral Seas), the Turgai Depression (the northern Kazakhstan), Miocene — in Europe and Northern Alaska; Pliocene–Pleistocene — in Europe, Iceland, Greenland, Canadian and Russian Arctic. Both Recent species of *Cyrtodaria* are known as fossils. The oldest late glacial ages available for *C. kurriana* are from the Western Canadian Arctic Archipelago (11.5 ¹⁴C ka BP) and the Laptev Sea (<10.3 ¹⁴C ka BP) (England, Fueze, 2008). If the abyssal occurrence of live *C. kurriana* is confirmed, *Cyrtodaria* will be the only abyssal genus known from the Arctic pre-Pliocene.

There are two extant genera, *Laubiericoncha* and *Saracrinus*, recorded in the Arctic abyssal as fossils but not known in the Recent Arctic fauna. The fossil valves of *Laubiericon-*

cha sp. were collected at the Gakkel Ridge (77°46'2" N 126°07'2" E, 1992–2054 m) (Sirenko et al., 1995; Krylova, Sahling, 2010; Krylova et al., 2011). The age was estimated about 15.7 kyr (late Pleistocene) (Sirenko et al., 1995). The genus *Laubiericoncha* includes four species known from low and temperate latitudes of the Pacific and Atlantic Oceans at depths from 1323 to 3159 m (Krylova, Sahling, 2010) all restricted to sulphide-rich reducing environments. A fragment of stalk of the crinoid *Saracrinus* sp. was found in the Canada Basin (the drifting station North Pole-22, St. 29, 26.07.1977, ~80°N, 128°E, 2630–2910 m) (Afanasjev, Filatova, 1980; Klikushin, 1992). The age of the fragment was not identified. Good preservation of relief on the columnal articulate surface indicates a probable young (?Pleistocene) age. The genus *Saracrinus* belongs to the family Isselocrinidae (Klikushin, 1977). The family is known from the Upper Cretaceous deposits (Hess, 2011). Presently Isselocrinidae occur mostly at low latitudes. The species *Endoxocrinus* (*Diplocrinus*) *wyvillethomsoni* is the most deep-water and most northern in the family, it occurs from Morocco to the Bay of Biscay at depths from 1246 to 2070 m. It can be suggested that the stalked crinoids of the family Isselocrinidae were present in pre-Pliocene Arctic deep-sea fauna but became extinct.

7. Arctic emergence

In the present study the “emergence” and “submergence” of fauna are considered from the viewpoint of historical biogeography. We use the terms emergence and submergence to designate trends in faunal dispersal during the Pliocene–Pleistocene colonization of the Arctic Ocean. “Emergence” corresponds to the rise of fauna from deeper waters to shallower depths and the opposite trend is “submergence” (descent).

Shorygin (1928) showed that several species of echinoderms occur in the Arctic at shallower depths than in the North Atlantic. For example, the upper boundary of occurrence of

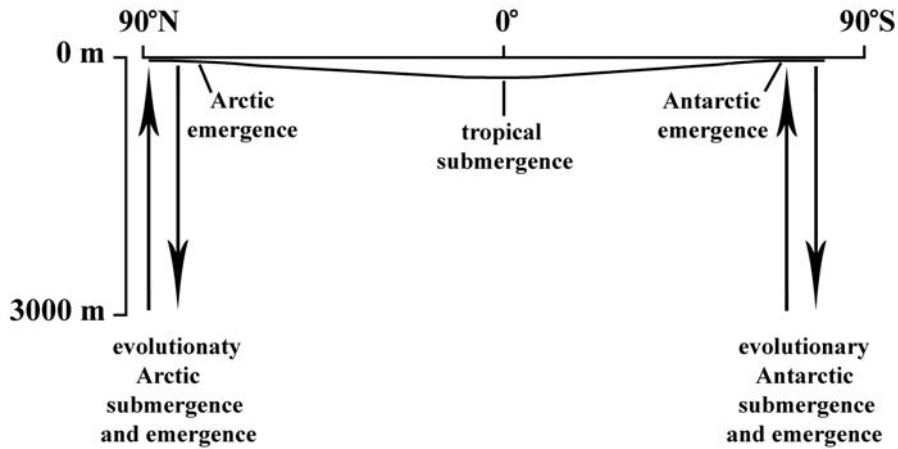


Fig. 2. Sketch of polar emergence/tropical submergence in the distribution of a taxon and the evolutionary polar emergence/polar submergence in biogeographical history of a taxon. The curve shows the upper limits of the bathymetrical ranges of a taxon. Vertical rows show two opposite vectors of vertical dispersal of polar faunas in the Pliocene and the Pleistocene.

Рис. 2. Схематическое изображение полярной эмергенции/тропической субмергенции в распространении таксона и эволюционной полярной эмергенции/полярной субмергенции в биогеографической истории таксона. Кривая линия показывает верхний предел вертикального распространения таксона. Вертикальные стрелки показывают два противоположных направления распространения по вертикали полярной фауны в плиоцене и плейстоцене.

the abyssal *Ophiacantha bidentata* near the southern range border is at the depth 800 m, in the middle of boreal zone at 200–300 m, in the northern boreal at 100 m, in the low Arctic at 10–25 m and in the high Arctic at 5 m (Shorygin (1928). This phenomenon was called the “boreal submergence” by Ekman (1953). Ekman considered the boreal submergence as a particular manifestation of a broader phenomenon — the equatorial submergence: when a species or a genus at high latitudes occurs in shallow waters and appears at greater depths at low latitudes. The term “submergence” has been introduced by Häcker (1904) who pointed to this tendency in pelagic radiolarians. The equatorial or tropical submergence usually is explained by the influence of temperature and illumination on vertical distribution of animals (Sverdrup et al., 1942; Ekman, 1953; Schmitt, Kott, 1969; Hessler, 1970b). Cold-water animals need colder, deeper waters in regions with warm surface water (Ekman, 1953: 249).

Based exclusively on chorological (bathymetric) characteristics, Ekman’s phenomenon of boreal submergence can be designated as the “Arctic emergence”. In other words, one and the same phenomenon can be described in different terms depending on the point of view. Bathymetric patterns of a taxon in the Arctic Ocean and the North Atlantic can be compared in terms of the Arctic emergence (Filatova, Zenkevitch, 1957; Zenkevitch, 1963; Shchedrina, 1964; Svarsson et al., 1993; Kosobokova, 2010). Thus, according to Zenkevitch (1963: 63) many members of the abyssal fauna of the Arctic Basin have risen into the comparatively shallow zones along its fringes in seas with Arctic conditions. Zenkevitch explained the Arctic emergence of some taxa by the following four reasons: (1) lower temperature of surface water in the high Arctic, (2) small annual temperature fluctuations, (3) comparatively low transparency of water and (4) obscuration caused by the ice cover lasting almost the year round.

Table 5. Species of asselote isopods with an upper depth boundary in the Arctic Ocean shallower than in the North Atlantic. All species belong to the Arctic abyssal genera. The difference between the Arctic and Atlantic minimum depths is more than 100 m. After Svavarsson et al. (1993, Table 1), except for depth values marked by asterisk.

Таблица 5. Виды асселотных изопод, у которых верхний предел распространения в Северном Ледовитом океане расположен на меньших глубинах, чем в Северной Атлантике. Все виды принадлежат к арктическим абиссальным родам. Разница между минимальными глубинами обитания в Северном Ледовитом океане и Атлантике более 100 м. По Svavarsson et al. (1993, Table 1), за исключением глубин, помеченных звездочкой.

Species	Depth range, m	
	Within the Arctic Ocean	Within the North Atlantic
<i>Desmosoma lineare</i>	17–531	172–1564*
<i>Disconectes furcatus</i>	150–350	390*–2258
<i>Disconectes phalangium</i>	54–681	478–1597
<i>Eugerdella coarctata</i>	24–350	2702
<i>Eurycope brevirostris</i>	160–1501	1505–3423*
<i>Eurycope inermis</i>	200–2380	682–1518
<i>Eurycope producta</i>	72–2681*	309–2087
<i>Gracilimesus angustus</i>	698–1373	2137
<i>Haplomesus quadrispinosus</i>	365*–3672	2258–4150
<i>Haploniscus ingolfti</i>	854–2465	2892*–4100
<i>Ilyarachna hirticeps</i>	20–3270	2239–2496
<i>Ilyarachna longicornis</i>	8–3824*	364–5223
<i>Ischnomesus bispinosus</i>	10–537	344*–1100
<i>Macrostylis spinifera</i>	4–681	542*–1760
<i>Macrostylis subinermis</i>	830–2105	2800*–3474
<i>Munna acanthifera</i>	60–3709	584–2258
<i>Munna boeckii</i>	37–188	320–350
<i>Munna hansenii</i>	90–1020	913–1505
<i>Oecidiobranchnus plebejum</i>	80–1666	1330–1610
<i>Rapaniscus crassipes</i>	219–457	1300–2754
<i>Whoia angusta</i>	50–680	824–2500

When bathymetric patterns are considered from the viewpoint of historical biogeography, the terms submergence and emergence designate two different events: dispersal of fauna from the shelf to the deep sea and dispersal in the opposite direction (Fig. 2). In evolution of faunas, emergence and submergence should be discussed in terms of historical factors but not peculiarities of the modern environment (see below).

The Arctic species (including those with the Arctic-boreal distribution) occur shallower than non-Arctic species in 39 (42%) abyssal genera (Table 1). Among those genera, in 24 the difference between the minimum depth of occurrence in the Arctic and non-Arctic species is >100 m. There is also difference between the minimum

depth of occurrence at the intraspecies level (Table 5).

The probability of evolutionary Arctic emergence is highest for 12 abyssal genera. They include *Ilyarachna* and *Pourtalesia*, the classic examples of evolutionary emergence of the deep-sea fauna (Hessler, Thistle, 1975; Mironov, 1975, 2008; Hessler et al., 1979). *Ilyarachna* is the most speciose (41 species) and the most eurybathic (8–7230–?10687 m) genus in the subfamily Ilyarachninae, family Munnopsidae. Recent molecular studies supported the hypothesis of the deep-sea origin of *Ilyarachna*. According to 18S and 28S Bayesian analyses, *Ilyarachna* forms a monophyletic group together with *Echinozone* and *Notopais*, whereas *Syneurycope* is suggested as their sister group

(Osborn, 2009; Raupach et al., 2009). The deep-sea distribution of the basal genus *Syneurycope* (1280–5122 m) suggests the deep-sea origin of *Ilyarachna*. This genus ascended to depths shallower 100 m in three areas: the Arctic Ocean (*I. longicornis*, minimum depth 8 m), the Southern Ocean (*I. nordenstami*, 50 m) and southern California (*I. acarina*, 80 m). Most species of this genus (28) occur at the depth exceeding 2000 m.

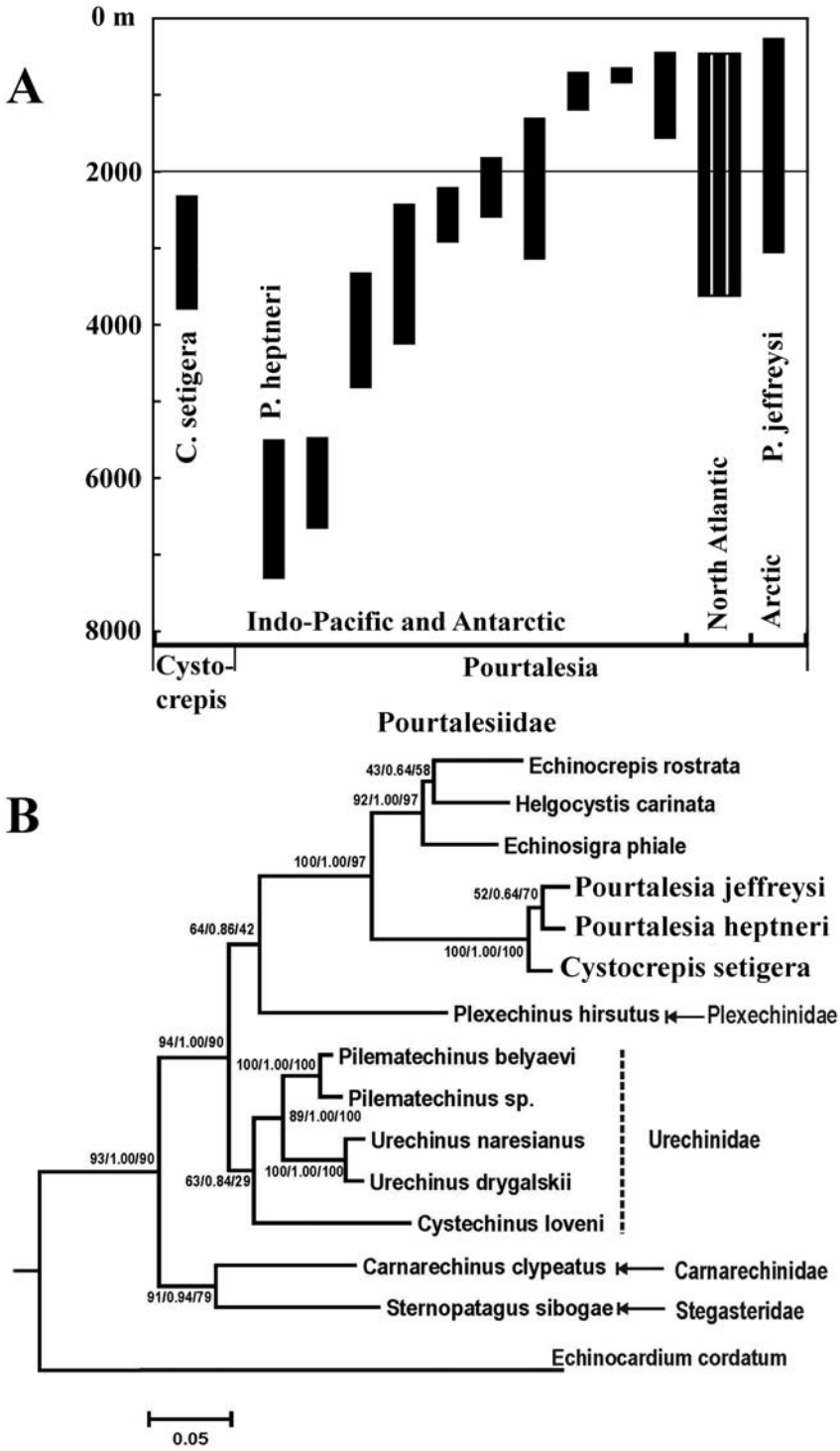
Pourtalesia is the most species-rich (12 species) and the most eurybathic (220–7340 m) genus in the family Pourtalesiidae. Among nine genera of the family, only *Pourtalesia* was recorded at depths shallower than 1000 m. Shallow-water records were in the Arctic Ocean (*P. jeffreysi*, minimum depth 220 m), the North-West Pacific (*P. laguncula*, 227 m), the Southern Ocean (*P. aurorae*, 432 m) and the Caribbean (*P. miranda* sensu stricto, 450 m). Most species of the genus occur at depths exceeding 2000 m (Fig. 3). In the northern Atlantic the genus was not recorded shallower than 1000 m. Morpho-functional (Mironov, 1975, 1982, 2008) and molecular studies (Petrov et al., 2012) indicate the deep-sea origin of *Pourtalesia*. Mironov (op.cit.) grouped genera of echinoids according to increasing morphological specialization to life within the deep-sea sediment. The least specialized genera show the most limited vertical and geographical distribution: they occur only in the abyssal of the Southern Ocean and the East and North Pacific. The most specialized genera are eurybathic and cosmopolitan, occurring from the upper bathyal to hadal worldwide, from the Southern Ocean to the Arctic. Only the most specialized genera (*Pourtalesia*, *Echinosigra* and *Solenocystis*) were found in the northern Atlantic and only the species *Pourtalesia jeffreysi* was reported from the Arctic Ocean. The following trend generally is common in the family Pourtalesiidae: the more advanced is a genus the broader is its vertical and geographical distribution (Mironov, 1975, 2008). Occurrence of *Pourtalesia* in the Arctic Ocean is an illustration of this trend.

The phylogeny of pourtalesiids, including the Arctic endemic *Pourtalesia jeffreysi*, based

on mitochondrial genes 16S rRNA and cytochrome oxidase (COI) 14 (Petrov et al., 2012) supports the evolutionary line from *Cystocrepis* to *Pourtalesia* (Mironov, 2008) and emergence of the abyssal fauna of pourtalesiids (Mironov, 1975). *Cystocrepis*, basal in this line, is not known shallower than 2000 m, whereas the advanced *Pourtalesia* ascends in the Arctic to 220 m (Fig. 3).

Global distribution patterns, similar to those in *Ilyarachna* and *Pourtalesia*, are common for a number of other genera: *Anthosactis*, *Eurycope*, *Gracilimesus*, *Haplomesus*, *Ischnomesus*, *Macrostylis*, *Pseudomesus*, *Amblyops*, *Bathycrinus*, *Elpidia*, *Kolga* and *Hymenaster*. These genera are widely distributed in the World Ocean and include many species occurring outside the Arctic Ocean (except for *Kolga*). They belong to mainly deep-sea families with a typical deep-sea distribution. The shallowest record in each of these genera is in the Arctic, the difference between the minimum depth of occurrence in the Arctic and elsewhere is more than 100 m. It can be suggested that genera with such a distribution pattern emerged in the Arctic Ocean.

The cosmopolitan genera *Macrostylis* (Isopoda) and *Elpidia* (Holothuroidea) demonstrate interesting examples of bipolar emergence (both in the Arctic and Antarctic). *Macrostylis* is the only genus in the family Macrostylidae. It includes 82 species and has the widest depth range among the isopod families (Riehl, Brandt, 2010; Riehl et al., 2012). The deepest record at 10730 m has been reported from the Mariana Trench (Mezhov, 1993). Most species (71, or 87%) were not recorded shallower 2000 m. Only the following eight species occur at depths <1000 m: *M. abyssicola* (Davis Strait and Kara Sea, 698–3921 m), *M. gerdesi* (Southern Ocean, Maud Rise, 238 m), *M. longipes* (Iceland, western Norway and the Canada Basin, 325–1412 m), *M. longiremis* (Skagerrak and west of Iceland, 149–228 m), *M. polaris* (outer Chukchi shelf, 325–340 m), *M. setulosa* (Southern Ocean, Scotia Sea, 757–2705 m), *M. spinifera* (North Atlantic, Norwegian Sea, 4–1761 m) and *M. subinermis* (Davis Strait, Norwegian and Green-



land Seas, north of Chukchi Sea, 830–3474 m). Thus, the genus shows a classical deep-sea distribution with records on the shelf or upper slope only in high latitudes in both hemispheres.

Elpidia (22 species, 70–9735 m) is the most widely distributed and eurybathic genus in the family Elpidiidae. All records of *Elpidia* at depths <1000 m are in the Arctic Ocean (minimum depth 70 m) and the Southern Ocean (542 m). Morphological data suggest dispersal of *Elpidia* through the North Atlantic into the Arctic Ocean (Belyaev, 1975; Gebruk, 1990). Cladistic analysis, based on morphological characters, supports this hypothesis and indicates the Arctic emergence with formation of the most shallow-water species in the family, *Elpidia glacialis*, occurring at depths from 70 to 610 m (Rogacheva, 2007; Budaeva, Rogacheva, 2013; Rogacheva et al., 2013).

One and the same genera emerge both in the Arctic and the North Atlantic. For example, *Pourtalesia* ascends to 1160 m in the North Atlantic and 220 m in the Arctic, *Kolga* — to 1484 m and 659 m respectively. The Arctic emergence is not characteristic of small genera. *Kolga* is a rare example.

8. Arctic submergence

In 22 (24%) abyssal genera, the Arctic species (including records outside the Arctic Ocean) were found at greater depths than the non-Arctic species (Table 1). Among these genera, the

following occur only in the Arctic abyssal: *Oceanactis*, *Cryodesma*, *Saduria*, *Pseudomyxis*, *Portlandia*, *Tylaster*, *Ophiopleura* and *Dendrodoa*. Distribution patterns of the isopod *Saduria* and the ascidian *Dendrodoa* suggest, with a high probability, the Arctic shelf origin of abyssal species.

The genus *Dendrodoa* includes six species distributed in the Northern Hemisphere. The only species not known in the Arctic, *D. abbotti*, occurs in the north-east Pacific from the intertidal to 12 m (Newberry, 1984). The only species in this genus occurring in the abyssal is the Arctic-boreal *D. grossularia* (2340 m, the northern Laptev Sea). All other records of this species were from depths 6–600 m (Sirenko et al., 2004).

The distribution of *Saduria* similar to *Dendrodoa* is limited to the Northern Hemisphere (Fig. 4). There are four species in this genus: two Arctic endemics, *S. sibirica* (0–90–?160 m) and *S. megalura* (1546–3127 m), the Arctic-North Atlantic *S. sabini* (3–2298 m) and widely distributed in brackish and fresh waters glacial relict *S. entomon* (0.5–2681 m). The relict nature of *S. entomon* has been discussed by Segerstråle (1957): this species is common in Arctic estuaries, the Baltic and Caspian Seas and various northern inland lakes. Recently *S. entomon* invaded the Black Sea (Kvach, 2009). Records of *Saduria* deeper than 2000 m are known from the Norwegian, Greenland, Amundsen and Canada Basins (Sars, 1886; Gurjanova, 1946a; Malyutina, Kussakin, 1996a; Brandt, 1997a; De Broy-

Fig. 3. As example of Arctic emergence, the echinoid genus *Pourtalesia*.

A — bathymetric distribution of species of *Cystocrepis* and *Pourtalesia*; right bar — bathymetric range of the Arctic endemic *P. jeffreysi*; triple bar — bathymetric range of three closely related Atlantic species, now all recognised as *P. miranda*.

B — consensus phylogenetic tree of the order Holasteroidea based on COI, 16S and 12S sequences inferred from MP, BI and ML analyses with *Echinocardium cordatum* (order Spatangoida) as the outgroup. Numbers by nodes indicate bootstrap supports for corresponding clades. *P. heptneri* is the deepest species (5500–7340 m) and *P. jeffreysi* is the shallowest species (220–3081 m) in the genus. After Petrov et al. (2012).

Рис. 3. Пример арктической эмергенции, морские ежи рода *Pourtalesia*.

A — вертикальное распространение видов *Cystocrepis* и *Pourtalesia*; самый правый столбик — батиметрический диапазон арктического эндемика *P. jeffreysi*; тройной столбик — батиметрический диапазон трех близко родственных видов в Атлантике, объединенных под видовым названием *P. miranda*.

B — филогенетическое дерево отряда Holasteroidea, основанное на объединенных нуклеотидных последовательностях 16S, 12S и COI, полученных с помощью MP, BI и ML анализов, с *Echinocardium cordatum* (отряд Spatangoida) в качестве внешней группы. Цифры при узлах указывают поддержку для соответствующих клад. *P. heptneri* является наиболее глубоководным видом (5500–7340 м), и *P. jeffreysi* — наиболее мелководный вид (220–3081 м) в роде. По Петрову и др., (2012).

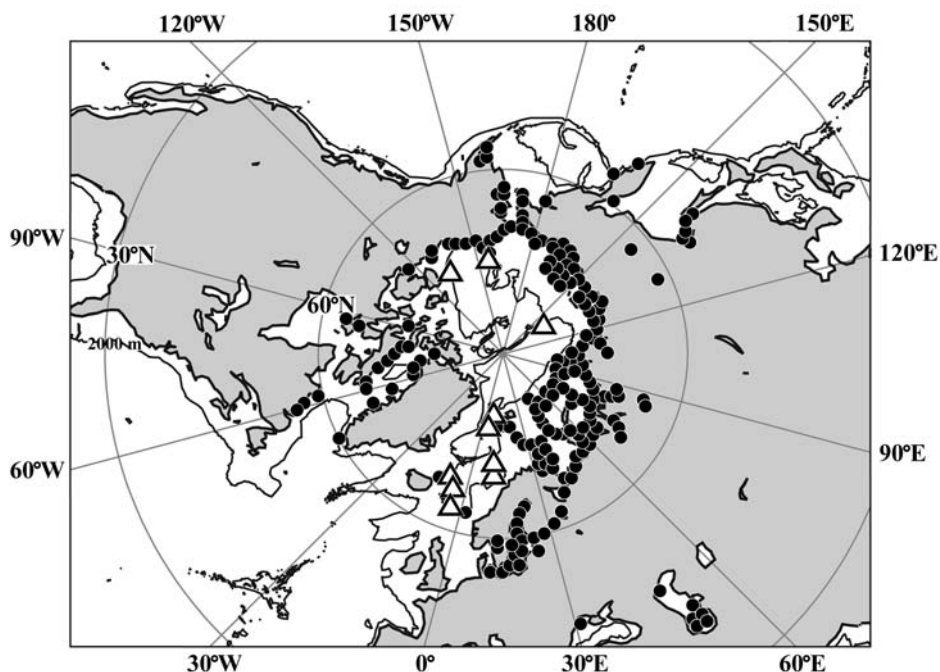


Fig. 4. Example of the distribution of an abyssal genus with an Arctic shelf origin: distribution of isopods of the genus *Saduria*; circles — records <2000 m; triangles — abyssal records (>2000 m). After Ekman (1953) and Guryanova (1985b) with additions.

Рис. 4. Пример распространения рода, абиссальная фауна которого имеет арктическое шельфовое происхождение: распространение изопод рода *Saduria*; кружочки — находжения на глубинах менее 2000 м; треугольники — находжения в абиссали (>2000 м). По Экману (1953) и Гурьяновой (1985b) с добавлениями.

er, Martin, 2004; Bergman et al., 2009; MacDonald et al., 2010). Morphological data suggest the shallow-water origin of the deep-sea endemic *S. megalura* (Gurjanova, 1946b, 1970). Both *Dendrodoa* and *Saduria* occur in a wide range of habitats. *D. grossularia* is known from wave-washed vertical infralittoral rocks to abyssal plains. *S. entomon* occurs from inland lakes to abyssal plains.

Fewer abyssal genera show Arctic submergence compared to Arctic emergence. The Arctic submergence is well pronounced only in two genera (2%) out of the 92 genera considered, whereas Arctic emergence is highly possible for 12 genera (13%). However, the share of genera with an Arctic submergence pattern substantially changes depending on taxon: from 0% (e.g. Echinoidea, Crinoidea, Holothuroidea) to about

25% (Amphipoda). The amphipod fauna is characterized by probably the highest percentage of genera with submergence from the Arctic shelf to the abyssal. At least 64 genera of Amphipoda are known in the Arctic abyssal. This list is most probably incomplete. Distribution patterns suggest an Arctic shelf origin of abyssal species in at least 16 genera (Table 2). Distribution patterns of these genera (except for *Ischyrocerus*) are similar to those in *Saduria* and *Dendrodoa*. Genera of presumably the shelf origin occur on the shelf both in the Arctic and outside it but are found in the abyssal only in the Arctic Ocean (except for *Ischyrocerus*). They are not known from the Southern Hemisphere (except for *Ischyrocerus*, *Haliragoides* and *Tmetonyx*) but a half or most of their species occur in the Arctic (except for *Ischyrocerus* and *Metacaprella*).

The genus *Ischyrocerus* deserves special attention. The distribution pattern of this genus suggests the Arctic shelf origin of abyssal species, despite the cosmopolitan distribution of the genus and occurrence in the abyssal outside the Arctic. The centre of species diversity is in the Arctic (17 species) and the North Pacific (18 species). The difference between tropical and northern species is so pronounced that Myers (1997) suggested splitting the genus. Among 17 Arctic species of *Ischyrocerus*, three occur in the Arctic abyssal. There is only one record of the genus in the abyssal outside the Arctic: *I. hortatory* was found off Isla de Chiloe (Chile) at 2454 m.

Genera listed in Table 2, similar to *Saduria* and *Dendrodoa*, are characterized by high adaptability. Representatives of these genera inhabit all the main types habitats found in the Arctic: marine and brackish-water, benthic and pelagic, algal beds, intertidal rocks and fine deep-sea silts. There are also commensals among these genera. Species of *Onisimus* and *Apherusa* together with other amphipods dominate the ice-associated (sympagic) fauna (Melnikov, 1997; Gradinger, Bluhm, 2004; Arndt, Pavlova, 2005; Macnaughton et al., 2007; Nygård, 2011). Various habitats of only one species, *Ischyrocerus anguipes*, common in intertidal and upper subtidal zones of northern regions include intertidal rocks at high tide (Ingólfsson, Agnarsson, 2003), medium and coarse sand, pebble (Vallet, Dauvin, 1995), laminarian beds (Ryżycki, Gruszczyński, 1986), macroalgal rafts (Thiel, Gutow, 2005), estuaries (Ardisson, Bourget, 1992; Anisimova, 2000) and biotopes beneath the ice (Arndt, Swadling, 2006). This species also was recorded as a symbiont of invading species. Thus, *I. anguipes* was reported as a symbiont of the red king crab *P. camtschaticus* shortly after the latter appeared in the Barents Sea (Dvoretzky, Dvoretzky, 2009). In the North Pacific *I. anguipes* is known in association with the invaded brown seaweed *Sargassum muticum* (Norton, Benson, 1983).

For some genera (e.g. the amphipods *Amphilochoopsis*, *Centromedon*, *Dulichlopsis* and *Unciola*) it is difficult to elucidate the region

(the Arctic or North Atlantic) where the primary descent to the abyssal took place: some abyssal records belong both to the Arctic and the northern Atlantic close to the boundary between the Arctic and the Atlantic. Abyssal records of some, mostly shallow-water, genera (e.g. the amphipods *Leptophoxus*, *Metopa* and *Plesymtes* and the isopods *Ananthura* and *Calathura*) are known only from the boundary zone between the Arctic and the Atlantic, including areas of the Davis Strait, south of Greenland, south and south-west of Iceland (Fig. 5).

The amphipods of the *Themisto* genus were considered as mainly epipelagic, although some specimens have been recorded at depths 2000–3000 m (Vinogradov et al., 1982). Bulycheva (1964) reported *Themisto abyssorum*, *T. compressa* (the junior synonym of the Antarctic *T. gaudichaudii*) and *T. libellula* from the Arctic Ocean deeper than 2000 m (down to 3000 or 3100 m). Dense near-bottom populations of *T. abyssorum* (mainly the near-adult females) were observed on dives of the *Mir* submersibles in the Norwegian Sea at 1200–1700 m (Vinogradov, 1999). Bulycheva (1964) suggested that *T. compressa* drifts with the Gulf Stream from the North Atlantic to the Central Arctic and the Barents Sea. If so, *T. compressa* in the Arctic may occasionally descend from shallow waters to the deep-sea.

Genera characterized by Arctic submergence have penetrated the Arctic shelf from the shelf of the North Atlantic or North Pacific. The first pathway seems to be common for most genera. Only in *Arrhis*, *Ischyrocerus* and *Metacaprella* do most species occur in the North Pacific. Therefore, it is most likely that they have dispersed from the North Pacific shelf.

The biogeographical history of the Arctic Ocean is characterized by active processes of emergence and submergence. Perhaps only the Southern Ocean is comparable with the Arctic in intensity of evolutionary emergence and submergence of fauna. Some authors suggest (Gurjanova, 1939, 1957; Koltun, 1964; Nesis, 1983, 2001; Svavarsson et al., 1993; Clarke, 2003) that part of shallow-water Arctic fauna survived during the glaciation owing to migration to the

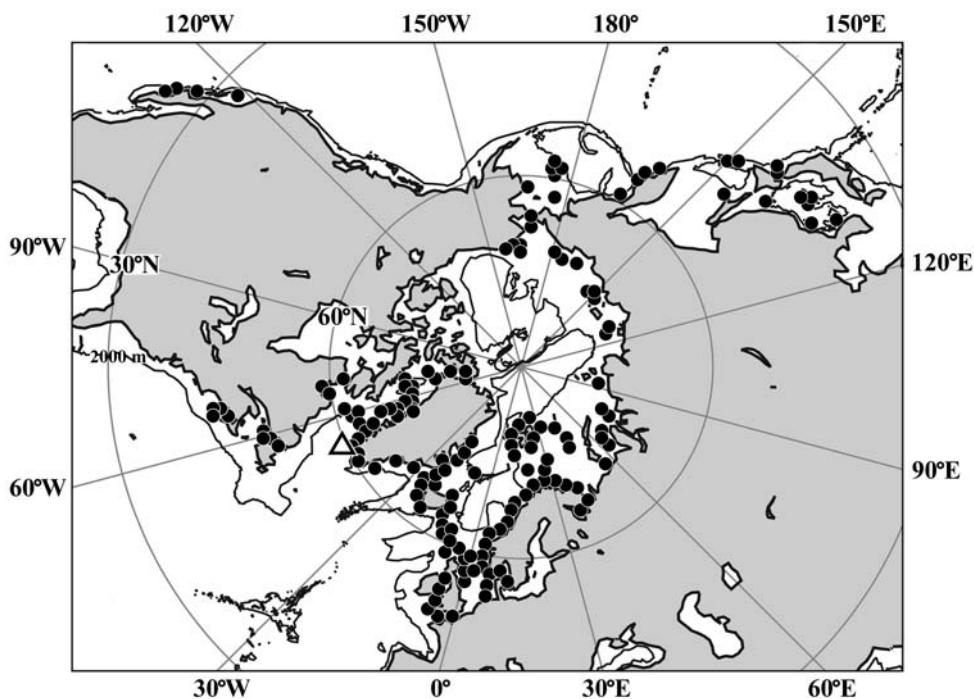


Fig. 5. Distribution of amphipods of the genus *Metopa*. A single abyssal record is in the transition zone between the arctic and boreal faunas. Circles — records <2000 m, triangle — abyssal record (3521 m). After Tandberg (2011) with additions.

Рис. 5. Распространение амфипод рода *Metopa*. Единственное нахождение в абиссали расположено в переходной зоне между арктической и boreальной фаунами. Кружочки — находения на глубинах менее 2000 м, треугольник — нахождение в абиссали (3521 м). По Tandberg (2011) с добавлениями.

Arctic Ocean depths. However, this hypothesis cannot explain the fact that together with submergence there was an active emergence of deep-sea fauna in the Arctic Ocean. Besides, the increase of extent and thickness of the ice sheet during periods of glaciation should have led to depression of both shallow-water and deep-sea faunas: surface productivity declined and water stratification intensified resulting in decline of organic matter and oxygen at depths.

The Arctic submergence and emergence are apparently caused by the same factors: the similarity of shallow-water and deep-sea environments in the Arctic Ocean and the young age of the modern Arctic environment (and Arctic biotic complexes). If so, the emergence and submergence occurred in the Arctic simultaneously and followed similar scenarios. The Arctic

fauna was depressed during glaciations, resulting in a decrease of species diversity and destruction of the biotic complexes. The post-glacial warming stimulated dispersal of deep-sea and shallow-water species into the Arctic Ocean from the donor regions, the North Atlantic and the North Pacific. The deep-sea and shallow-water environments in the Arctic are less different than in the donor regions. This can stimulate dispersal both from and to the deep. In addition, the pre-glacial biotic complexes of the Arctic Ocean were destroyed and barriers to dispersal became more easily permeable (Mironov, 2013). As a result, some deep-sea genera dispersed to shallow waters (the Arctic emergence), whereas other genera dispersed from shallow waters to the deep (the Arctic submergence).

Acknowledgements

We are grateful for advices on the abyssal species distribution to the following experts: N. Sanamyan (Actiniaria), K. Sanamyan (Ascidia), M. Malyutina (Isopoda), G.M. Vinogradov, and O.E. Kamenskaya (Amphipoda), A.V. Gebruk (Holothuriodea). This work is part of the project “Arctic marine fauna: data accumulated in Russia” (sub-project of the CoML “Arctic Ocean Diversity” program).

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