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The ratio of species of Atlantic and Pacific origin in modern Arctic fauna of bivalve molluscs

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ABSTRACT. The present work aims to estimate the ratio of species of the bivalve molluscs of the Atlantic and the Pacific origin in different geographical and bathymetrical regions of the Arctic basin. Seven shallow-water regions of the Arctic, with depths of 0–300 m, (the Norwegian, Barents, Kara, Laptev, East Siberian, Chukchi and Beaufort Seas) and three deep-sea regions with depths exceeding 1000 m (the Norwegian and Greenland Basins, Nansen and Amundsen Basins, Canada Basins) are considered. For the identification of origin we combined fossil records with records of the distribution of living genera and, when possible, used molecular genetic data. The distribution patterns of 265 species from 132 genera were analysed.
The share of species of Atlantic origin decreases in marginal Eurasian seas from the Norwegian Sea to the Chukchi Sea, and then increases in the Beaufort Sea. The share of species of Pacific origin is higher only in the Chukchi and Beaufort Seas, the species of the Atlantic and the Pacific origin are equally represented in the East-Siberian Sea. The share of species of the Atlantic origin is much higher in all deep-sea regions.
Many taxa of bivalves that dispersed into the Arctic from the North Pacific also penetrated into the North Atlantic. In contrast, most taxa of the Atlantic origin remained in the Arctic Ocean, having stopped at the Bering Strait. Differences between the Arctic boundaries, the Arctic - Atlantic (the Greenland-Iceland- Faeroe Ridge) and the Arctic - Pacific (the Bering Strait) as barriers for dispersal are discussed.

KEY WORDS: Arctic Ocean, biogeography, Bivalvia, origin of fauna.

Соотношение видов атлантического и тихоокеанского происхождения в современной арктической фауне двустворчатых моллюсков

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РЕЗЮМЕ. Цель работы заключалась в оценке доли видов двустворчатых моллюсков атлантического и тихоокеанского происхождения в разных географических районах Арктики и на разных батиметрических горизонтах. Для анализа были выбраны 7

мелководных районов Арктики с глубинами от 0 до 300 м: моря Норвежское, Баренцево, Карское, Лаптевых, Восточно-Сибирское, Чукотское и Бофорта, и 3 глубоководных района с глубинами более 1000 м: Норвежская и Гренландская котловины, котловины Нансена и Амундсена, а также Канадская котловина. Всего проанализировано распространение 265 видов из132 родов. Вывод о районе вселения в Арктику для каждого рода был сделан на основе палеоданных, данных о современном распространении, а также были использованы опубликованные результаты молекулярных исследований.
Доля видов атлантического происхождения уменьшается в краевых морях от Норвежского до Чукотского моря, а затем несколько повышается в море Бофорта. В мелководных районах доля видов тихоокеанского происхождения превышает долю видов атлантического происхождения только в Чукотском море и море Бофорта; в Восточно-Сибирском море виды атлантического и тихоокеанского происхождения представлены равными долями. В глубоководных котловинах доля видов атлантического происхождения значительно превышает долю видов тихоокеанского происхождения.
Большая часть родов двустворчатых моллюсков, проникших в Арктику из Северной Пацифики, распространилась также и в Северной Атлантике. Напротив, большая часть родов атлантического происхождения осела в Арктическом океане и не преодолела Берингов пролив, не приняв участия в трансарктическом обмене. Обсуждаются различия между барьерными свойствами границ Арктика-Атлантика (Гренландско-Исландско-Фарерский порог) и Арктика-Пацифика (Берингов пролив).

КЛЮЧЕВЫЕ СЛОВА: Арктика, биогеография, двустворчатые моллюски, происхождение фауны.

Introduction

The present Arctic fauna has been mainly shaped by repeated migrations of species from the Pacific and the Atlantic. The migrations were strongly influenced by glacial events and were most intense during periods of warming and the opening of the Bering Strait. As Dodson et al. (2007) pointed out, patterns of dispersal and colonization through the Bering Strait were complex, covering long periods of time and repeated Bering Strait openings. At least four openings are now documented. Fossil-calibrated dates indicate the openings during the early-mid Miocene ~16–17 million years ago (Ma), at the end of the middle Miocene ~11–12 Ma (Sher, 1999), near the end of the Miocene ~5.3 Ma (Gladenkov et al., 2002; Gladenkov, Gladenkov, 2004), and in the Pliocene between 4.1 and 3.1 Ma (Marincovich, Gladenkov, 1999). An intense trans-Arctic faunal exchange started only after the fourth opening of the Bering Strait, at approximately 3.1 Ma (Dodson et al., 2007; Vermeij, 1991). During subsequent glacial and interglacial periods the Arctic fauna retreated to the south and then repeatedly invaded northern regions.

There is an agreement among authors that the predominant direction of the trans-Arctic exchange of faunas was from the North Pacific towards the North Atlantic (Soot-Ryen, 1932; Ekman, 1953; Nesis, 1963; MacNeil, 1965; Durham, MacNeil, 1967; Kafanov, 1974, 1979, 1987; Gladenkov, 1978; Vermeij, 1991). At the same time, there is a serious discrepancy about the relative role of taxa of Pacific and Atlantic origin in the modern Arctic fauna. Among different groups of benthic invertebrates, echinoderms have been studied in most detail as to their ocean of origin. Considering the Arctic echinoderms as a whole, Anisimova (1986) and Smirnov (1994) incline to the opinion that the

Table 1. Cruises used as a source of material in the present work.
Таблица 1. Рейсы, материалы которых были использованы в работе.

Research Vessel	Cruise	Year	Area of study	Number of stations with studied material
Sevastopol	5	1957	Norwegian Sea, 105–1690 m	12
Sevastopol	8	1958	Norwegian Sea, 185–1860 m	5
Sevastopol	10	1958	Norwegian Sea, 140–1950 m	3
Sevastopol	15	1959	Norwegian Sea, 1000–1940 m	4
Vodnik, RT-61	26	1968	Barents Sea, 85–250 m	3
Persey-3	14	1975	North-Western Atlantic, 70–280 m	8
Tunets	105	1978	Barents Sea, 245–250 m	2
Dmitrii Mendeleev	49	1993	Kara Sea, 63–236 m	5

modern Arctic fauna is mainly of the Atlantic origin. Based on the fauna of starfish, Djakonov (1945) and Mironov and Dilman (2010) arrived at the conclusion that the North Pacific was the principal donor for shallow-water regions. For the deep-sea Arctic starfish it was shown that the half of the present genera are of Atlantic origin and another half of Pacific origin (Dilman, 2009). For other taxa, a predominantly Pacific genesis was suggested for fish (Andriyashev, 1939) and gastropods (Galkin, 1955), and a predominantly Atlantic origin for isopods (Kussakin, 1979).

Different opinions have been expressed on the origin of Arctic bivalves. Nesis (1965) and Kafanov (1974) suggested that the great majority of genera on the Arctic shelf are of Pacific origin. According to Filatova (1957a), the modern fauna of the Arctic bivalves has been mainly formed by species of Atlantic origin and autochthonous species. Fedyakov and Naumov (1987) supposed that more than a half the Arctic species are of Atlantic origin. Sirenko (2001) also believed that the impact of the Atlantic on the faunistic composition of Arctic Eurasian seas was higher than that of the Pacific. Some authors agree that the deep-sea Arctic bivalve fauna has Atlantic roots (Filatova, 1957a; Fedyakov, Naumov, 1987), however Bouchet and Warén (1979, tabl.3) found evidence of close relations of abyssal Arctic bivalves with the Pacific.

Although the origin of the recent Arctic bivalve fauna has been widely discussed, the relative importance of the Pacific and Atlantic elements in different Arctic regions remains mainly unknown. In the present paper we estimate the contribution of species of Pacific and Atlantic origin to the recent fauna of bivalves in different geographical and bathymetric regions of the Arctic. The origin of particular species was identified based on the biogeographical history of a genus. For the identification of origin, we use a complex approach combining fossil data with recent distribution of genera, and where possible the results of molecular genetics.

Material and Methods

Definition of regions

The boundaries of the Arctic Ocean are considered as passing along the northern limit of Davis Strait and the Greenland-Iceland-Faeroe Ridge, with the Atlantic and the Bering Strait, separating the Arctic and Pacific (Leontjev, 1985). These geomorphological limits of the Arctic do not coincide with biogeographic boundaries (Briggs, 1995, figs. 82–86). Our biogeographic analysis was based on seven selected shallow-water regions of the Arctic, with depths of 0–300 m, and three deep-sea regions with depths exceeding 1000 m. The shallow water regions include the Norwegian, Barents, Kara, Laptev, East Siberian, Chukchi and Beaufort Seas. The deep-sea regions include the western basins (Norwegian and Greenland Basins), the central basins (Nansen and Amundsen Basins) and the Canada Basin. Latitude 40ºN was taken as the southern border of the North Atlantic and the North Pacific for the purposes of this study.

Species considered

In this paper we use the term "Arctic species" for all species occurring in the Arctic Ocean without regard to a species range type. The list of Recent Arctic bivalve molluscs and data on their distribution was based mainly on literature sources: Gorbunov, 1946; Filatova, 1957a, b; Gladenkov, 1978; Bernard, 1979; Bouchet, Warén, 1979; Kafanov, 1979; Knudsen, 1985; Lubinsky, 1980; Fedyakov, Naumov, 1989; Warén, 1989, 1991; Brattegard, Holthe, 1997; Hansson, 1998; Gulliksen et al., 1999; Coan et al., 2000; Richling, 2000; Galkin, Voronkov, 2001; Sirenko, 2001; Kantor, Sysoev, 2005; Schiøtte, 2005; Sneli et al., 2005; Naumov, 2006; Sirenko et al., 2009; and others. Despite considerable gaps in the taxonomy and diversity of the Arctic bivalves, a significant step forward was made recently owing to the database efforts of the Zoological Institute of the Russian Academy of Sciences (www.zin.ru/projects/arccoml/eng/dbases.htm). For information about taxonomic composition and distribution of bivalves from the northern Atlantic and the Pacific, we used the WoRMS Database (Appeltans et al., 2012) and the Database of Western Atlantic Marine Mollusca, together with literature sources (Coan et al., 2000; Scarlato, 1981; Scarlato, Kafanov, 1988). We also used original data obtained by the authors, based on material collected on the cruises listed in Table 1. The genera used in the Bivalvia are not consistent between different sources. Mainly we followed WoRMS but in some cases accepted other versions closest to our own opinions.

The final list of the bivalve taxa from the studied regions contains 265 species from 132 genera.

The total number of species common with the North Atlantic, the North Pacific, and the number of Arctic endemics were calculated for each of the seven shallow-water and three deep-sea Arctic regions (Table 2; Figs 1, 2).

Data on the paleo-distributions was retrieved from the Paleobiology Database (http://paleodb.org/), as well as from numerous literature sources (Gladenkov, 1978; Kafanov, Ogasawara, 2003, 2004; Merklin et al., 1962, 1979; Svitoch, 2003 and others) and also from the database on bivalve molluscs of the European Neogene of R. Janssen (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt a. M.). We used data on fossil records, mainly from the northern regions of Europe, Asia and the North America, since the middle Miocene (Table 3). Overall 111 Recent genera (83% of the modern Arctic fauna) are known from fossil findings in the northern regions.

The source of bivalves penetrating into the Arctic Ocean

By characterizing genera as of North Pacific or North Atlantic origin, we mean not the region of origin of the genus but the region from which the genus first penetrated the Arctic Ocean.

The source region (Atlantic or Pacific) was suggested by the biogeographical history of the genus. If a genus migrated from the North Pacific to the North Atlantic through the Arctic and then a species of this genus colonised the Arctic from the North Atlantic, it was accepted that this species (and the genus) is of the North Pacific origin. If an endemic Arctic species belonged to a genus of Atlantic or Pacific origin, then this species was accepted as being from the Atlantic or Pacific correspondingly. "Dual" origin of a genus, i.e. migration of the genus to the Arctic independently from the Pacific and the Atlantic, was adopted only if supported by paleo-data at the species level.

The conclusions about origin were made for each individual genus based on paleontological and neontological evidences. Both paleontological and neontological data provide only indirect evidence the colonisation pathway, only suggesting that one of the two pathways is more probable. Therefore there is a high probability of incorrect conclusions about the colonisation pathway of some genera. Nevertheless, analysis of numerous taxa increases the chance of revealing real trends in the biogeographical history of the Arctic.

In paleo-analysis, data on the Recent Arctic species, or species closely related to them, were

Table 2. Number of Arctic bivalve species of different distributions and origins.
Таблица 2. Число видов арктических двустворчатых моллюсков с различным типом распространения и происхождения.

Region	Species numbers								
	species numbers	Arctic endemics	number of species common to the North Atlantic and/or North Pacific			Different regions of origin of Arctic bivalves			
			North Atlantic	North Pacific	North Atlantic + North Pacific	North Atlantic	North Pacific	Autochthonous	Indet
Norwegian Sea (<300 m)	193 (100%)		148 (76.5%)	1 (0.5%)	44 (23%)	164 (85%)	24 (12%)		5 (3%)
Barents Sea (<300 m)	99 (100%)	1 (1%)	44 (44%)	7 (7%)	47 (48%)	67 (68%)	29 (28%)		3 (4%)
Kara Sea (<300 m)	68 (100%)	2 (3%)	18 (27%)	7 (10%)	41 (60 %)	41 (60%)	25 (37%)		2 (3%)
Laptev Sea (<300 m)	65 (100%)	3 (5%)	18 (28%)	10 (15%)	34 (52%)	36 (55%)	26 (40%)		3 (5%)
East-Siberian Sea (<300 m)	59 (100%)	1 (2%)	10 (17%)	10 (17%)	38 (64%)	28 (48%)	28 (48%)		3 (4%)
Chukchi Sea (<300 m)	72 (100%)	3 (4%)	4 (6%)	26 (36%)	39 (54%)	24 (33%)	44 (61%)		4 (6%)
Beaufort Sea (<300 m)	61 (100%)	1 (2%)	7 (10%)	17 (27%)	36 (61%)	26 (44%)	32 (52%)	1(1%)	2 (3%)
Norwegian and Greenland Basins (> 1000 m)	24 (100%)	3 (13%)	11 (46%)		10 (41%)	19 (79%)	3 (12.5%)		2 (8.5%)
Nansen and Amundsen Basins (> 1000 m)	12 (100%)	4 (33%)	5 (42%)		3 (25%)	10 (83%)	1(8.5%)		1(8.5%)
Canada Basin (> 1000 m)	12 (100%)	6 (50%)	5 (42%)	1 (8%)		10 (83%)			2 (17%)

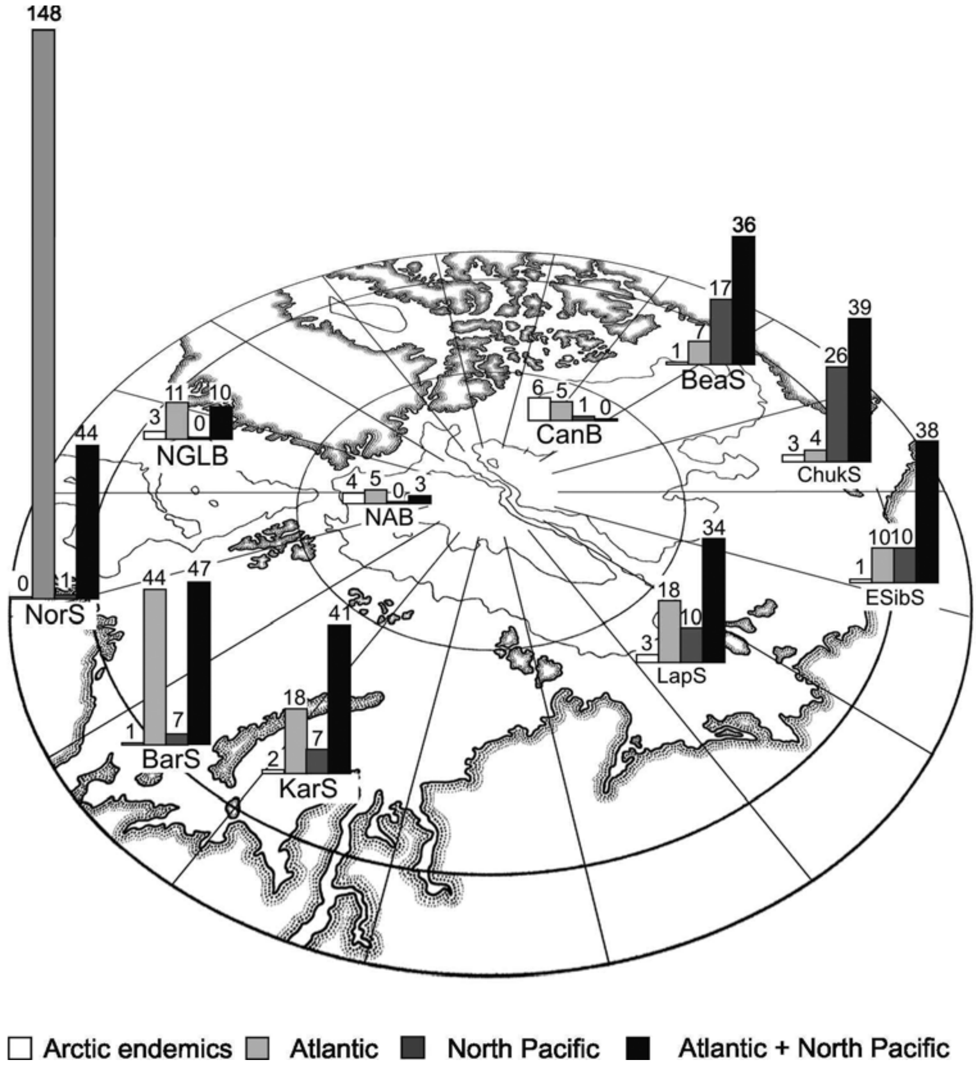


Fig. 1. Number of species of Bivalvia common with the North Atlantic and/or the North Pacific in different Arctic regions.

Abbreviations: NorS — Norwegian Sea; BarS — Barents Sea; KarS — Kara Sea; LapS — Laptev Sea; ESibS — East Siberian Sea; ChukS — Chukchi Sea; BeaS — Beaufort Sea; NGLB — Norwegian and Greenland Basins; NAB — Nansen and Amundsen Basins; CanB — Canada Basin.

Рис. 1. Число видов двустворчатых моллюсков общих с Северной Атлантикой и (или) северной частью Тихого океана в различных регионах Арктики.

Обозначения: NorS — Норвежское море; BarS — Баренцово море; KarS — Карское море; LapS — море Лаптевых; ESibS — Восточно-Сибирское море; ChukS — Чукотское море; BeaS — море Бофорта; NGLB — Норвежская и Гренландская котловины; NAB — котловины Нансена и Амундсена; CanB — Канадская котловина.

taken into account first. If data on a Recent Arctic species was absent, information on all species in the genus was examined. Paleo-analysis was performed by two approaches, differing by the length of the period covering the paleo-data. In the first, the period from the Middle Miocene to the present time was considered. In the second, the period considered was from the Pliocene to the present. The first version could overestimate the number of genera of

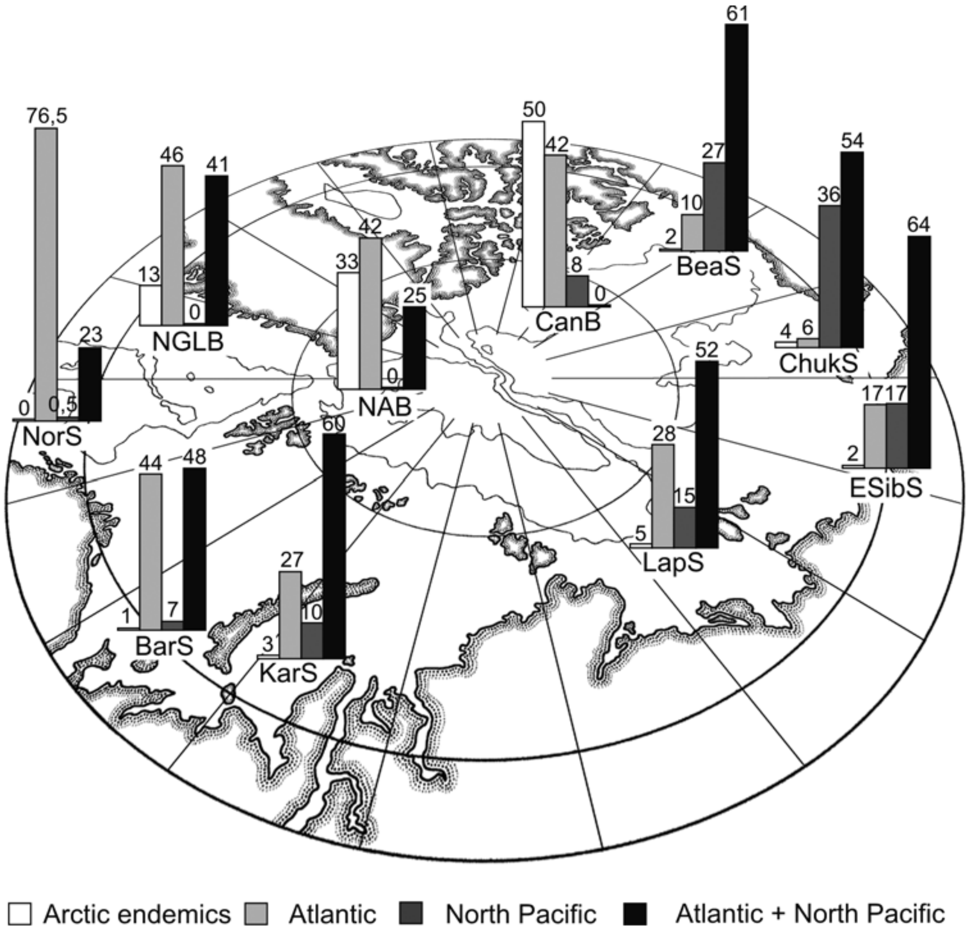


Fig. 2. Percentage of species of Bivalvia common with the North Atlantic and/or the North Pacific in different Arctic regions.
Abbreviations: see Fig. 1.
Рис. 2. Процентное соотношение видов двустворчатых моллюсков общих с Северной Атлантикой и (или) северной частью Тихого океана в различных регионах Арктики.
Обозначения те же, что на рис. 1.

Atlantic origin, because the Mediterranean Centre of Species Diversity (Mironov, 2006) still existed in the Miocene and fauna exchange occurred mainly through the low-latitude areas, from the Atlantic to the Pacific (Mironov, 2006). The second approach probably reflects the situation more adequately, because active trans-Arctic exchange between faunas of the North Atlantic and the North Pacific began in the Middle Pliocene, i.e. about 3.1 Ma (Vermeij, 1991; Dodson et al., 2007). We assumed that a genus entered the Arctic from the area of its earliest record during the corresponding chosen period. If the record ages of a genus in the North Atlantic and the North Pacific were the same, and modern Arctic species of this genus are unknown in fossils, the region from where the genus penetrated the Arctic was considered as uncertain. There is principle possibility of a "dual colonization" scenario, i.e. when different species of the same genus have independently invaded the Arctic from the North Pacific and the North Atlantic without the trans-Arctic exchange. We accepted this scenario only for the

Table 3. Paleo-records of Recent genera represented in the Arctic Ocean and their inferred region of penetration into the Arctic (records north of the present 40ºN were mainly considered; if a species name is indicated, record corresponds to this specific species).

Таблица 3. Палео-нахождения современных родов арктических двустворчатых моллюсков и предполагаемый район проникновения в Арктический бассейн (в основном учитывались нахождения севернее параллели 40°N; если указано название вида, то нахождение относится именно к этому виду).

	Genus	Middle–Late Miocene	Pliocene	Pleistocene	Region of penetration with Miocene records considered	Region of penetration with Miocene records not considered	Region of penetration: final conclusion with Recent distribution included
1	*Abra*	Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967)	Atlantic	Atlantic	Atlantic
2	*Acanthocardia*	Belgium (*echinata*[a], Vandenberghe et al., 2005)	United Kingdom (*echinata*[a], Wood, 1850)	Poland (*echinata*[a], Makowska, 1986)	Atlantic	Atlantic	Atlantic
3	*Acesta*	Sakhalin (Kafanov, Ogasawara, 2003)	Japan (O'Hara, Nemoto, 1988)		Pacific	Pacific	Uncertain
4	*Aequipecten*	Poland (Studencka, 1994 as *Chlamys*); Belgium, Germany (Vandenberghe et al., 2005)	United Kingdom (Balson, 1990); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967); Spain (Vera-Peláez et al., 2004)	Atlantic	Atlantic	Atlantic
5	*Altenaeum*		Greenland (Funter et al., 2001)	Alaska (Allison, 1973); Greenland (Simonarson et al., 1998)	No data	Atlantic	Uncertain
6	*Arca*	Spain (*noae* Jimenez, Braga, 1993); Poland (*noae*, Studencka, 1994); Paratethys (*tetragona*[a], pers. com., R. Janssen); Sakhalin (Kafanov, Ogasawara, 2003)	United Kingdom (*tetragona*[a], Woods, 1850); Belgium (Marquet, 2002); North Pacific (Gladenkov, 1978)	Italy (Bellomo, 1993); North Pacific (Gladenkov, 1978)	Atlantic (for *tetragona*)	Atlantic (for *tetragona*)	Atlantic
7	*Arcopagia*		Belgium (Marquet, 2002)	United Kingdom (Norton, 1967)	No data	Atlantic	Atlantic
8	*Arctica*	Belgium (Herman, Marquet, 2007); Arctic Alaska (MacNeil, 1965)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002)	Poland (Makowska, 1986)	Atlantic	Atlantic	Atlantic
9	*Asperarca*	Paratethys, North Sea basin (*nodulosa*[a], pers. com, R. Janssen)		Italy (Remia, Taviani, 2005)	Atlantic	Atlantic	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

10	*Astarte* s.l.	Poland (Studencka, 1994); Germany (Wienrich, 1999)	United Kingdom (Woods, 1850); Northeast European region of Russia (Krylov, 2008); Gulf of Alaska, (MacNeil, 1965); Kamchatka (Gladenkov, 1978)	United Kingdom (Norton, 1967); Italy (Bellomo, 1993); Greenland (Simonarson et al., 1998); Alaska (Allison, 1973)	Atlantic	Uncertain	Atlantic
11	*Axinopsida*		Greenland (Funter et al., 2001)	Greenland (Simonarson et al., 1998); Alaska (Allison, 1973)	No data	Atlantic	Pacific
12	*Axinulus*	Germany (Wienrich, 1999)			Atlantic	No data	Atlantic
13	*Barnea* (*Barnea*)	Italy (Bernasconi, Robba, 1993	United Kingdom (Wood, 1850); Italy (Benvenuti, Dominici, 1992)		Atlantic	Atlantic	Atlantic
14	*Bathyarca*	North Sea basin (Janssen, 1984)	United Kingdom (Woods, 1850); Greenland (Funter et al., 2001); Belgium (Marquet, 2002)	Northeast European region of Russia (*glacialis*[a], Merklin et al., 1979); Greenland (Simonarson et al., 1998); Chukotka (Merklin et al., 1962)	Atlantic	Atlantic	Atlantic
15	*Boreacola*				No data	No data	Autochthonous
16	*Cardiomya*	North Sea basin (Janssen, 1984); Germany (Wienrich, 1999)	Belgium (Marquet, 2002); Japan (Amano et al., 2000)		Atlantic	Uncertain	Atlantic
17	*Cerastoderma*	Greece (Dermitzakis, Georgiades-Dikeoulia, 1987)	United Kingdom (Wood, 1850); Iceland (Norton, 1975); Italy Benvenuti, Dominici, 1992); Belgium (Marquet, 2002)	United Kingdom (Gladenkov, 1978, as *Cardium*); White Sea (Svitoch, 2003)	Atlantic	Atlantic	Atlantic
18	*Cetomya*	Germany (as *Poromya*, Wienrich, 1999)			Atlantic	*No data*	Uncertain
19	*Chamelea*	Italy (Marasti, 1973); Bulgaria (Popov et al., 1996)	Italy (Benvenuti, Dominici, 1992)	Spain (Vera-Peláez et al., 2004)	Atlantic	Atlantic	Atlantic
20	*Chlamys*	Japan (Gladenkov, 1979); Alaska (Marincovich,1983); Kamchatka (*albida*[a]; Kafanov, Ogasawara. 2004)	Iceland (Gladenkov, 1978); Kamchatka (Gladenkov, 1978)	Greenland (Bennike et al., 1994); Alaska (Allison, 1973)	Pacific	Pacific	Pacific

Table 3 (continuing)
Таблица 3 (продолжение)

21	*Ciliatocardium*	Alaska (Marincovich, 1983)	United Kingdom (Gladenkov, 1978, as *Clinocardium*); Northeast European region of Russia (*ciliatum*[a], Merklin et al., 1979); Kamchatka (Kafanov, Ogasawara, 2004);	Northeast European region of Russia (*ciliatum*[a], Merklin et al., 1979); Greenland (Simonarson et al., 1998); Alaska (Miller, Dobrovolny, 1959)	Pacific	Pacific	Pacific
22	*Clausinella*	Bulgaria (Popov et al., 1996)	Belgium (Marquet, 2002)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
23	*Cochlodesma*	Germany (Wienrich, 1999)	Greenland (Funter et al., 2001); Belgium (Marquet, 2002)	Greenland (Simonarson et al., 1998)	Atlantic	Atlantic	Atlantic
24	*Crenella*	Germany (Moths et al., 2010); Oregon (Moore, 1963)	Belgium (*decussata*[a], Marquet, 2002)	North Carolina (Ward, Blackwelder, 1987); Alaska (Allison, 1973); North Sea Basin (Meijer, 1993)	Uncertain	Atlantic	Atlantic
25	*Cuspidaria*	North Sea basin (Janssen, 1984); Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1879); Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
26	*Cyclocardia*	North Sea basin (Janssen, 1984); Alaska (Marincovich, 1983); Sakhalin (*crebricostata*[a], Kafanov, Ogasawara, 2003); Kamchatka (Kafanov, Ogasawara, 2004)	Belgium (Marquet, 2002); Alaska (Hopkins, MacNeil, 1960); Sakhalin (*crebricostata*[a], *ovata*[a], Kafanov, Ogasawara, 2003)	Alaska (Allison, 1973)	Pacific	Pacific	Pacific
27	*Cyclopecten*				No data	No data	Atlantic
28	*Cyrtodaria*	Belgium (Herman, Marquet, 2007)	Belgium (Marquet, 2002); Greenland (Funter et al., 2001); Nuvok, Alaska (MacNeil, 1965)	Northest European region of Russia (Merklin et al., 1979); Poland (Makowska, 1986); Greenland (Simonarson et al., 1998); Chukotka (Merklin et al., 1962)	Atlantic	Atlantic	Atlantic
29	*Dacrydium*	North Sea basin (Janssen, 1984); Poland (Studencka, 1994)			Atlantic	No data	Atlantic
30	*Delectopecten*	Japan (Takayasu, 1986); Oregon (Moore, 1963)	Belgium (Marquet, 2002)		Pacific	Atlantic	Pacific
31	*Devonia*				No data	No data	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

32	*Diplodonta*	North Sea basin (Janssen, 1984); Poland (*rotundata*, Studencka, 1994)	United Kingdom (Woods, 1850); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967); Japan (Hayasaka. 1962); Alaska (Allison, 1973)	Atlantic	Atlantic	Atlantic
33	*Dosinia*	Spain (*exoleta*[a], Jimenez, Braga, 1993); Belgium (*lupinus*[a], Vandenberghe et al., 2005); Oregon (*whitneyi*, Moore, 1963)	Belgium (*exoleta*[a], Marquet, 2002); Japan (Hayasaka, 1973)		Atlantic	Atlantic	Atlantic
34	*Ennucula*	Alaska (Merklin et al., 1962)	Northeast European region of Russia (*tenuis*[a], Merklin et al., 1979); Greenland (Funder et al., 2001); Northeast Pacific (Coan et al., 2000)	Northwest Atlantic (Richards, 1962); Iceland (Gladenkov, 1978); Northeast European region of Russia (*tenuis*[a], Merklin et al., 1979); Greenland (*tenuis*[a], Simonarson et al., 1998)	Pacific	Pacific	Pacific
35	*Ensis*	Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
36	*Epilepton*				No data	No data	Atlantic
37	*Gari*	Poland (Studencka, 1994)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002)	Italy (Bellomo, 1993); Japan (Hayasaka, 1962)	Atlantic	Atlantic	Atlantic
38	*Glossus*	Italy (Bernasconi, Robba, 1993); Poland (Studencka, 1994)	Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
39	*Glycymeris* (*Glycymeris*)	Spain (*bimaculata,* Jimenez, Braga, 1993); Poland (Studencka, 1994)	United Kingdom (*glycymeris*[a] Wood, 1950); Belgium (*glycymeris*[a], Marquet, 2002)	Iceland (*glycymeris*[a], Gladenkov, 1978); Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
40	*Goethemia*			Greenland (Bennike et al., 1994)	No data	No data	Atlantic
41	*Goodallia*	Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1879); Belgium (Marquet, 2002)	North Sea Basin (Meijer, 1993)	Atlantic	Atlantic	Atlantic
42	*Gouldia*	Italy (Marasti, 1973); Poland (Studencka, 1994); Germany (*minima*[a], Moths et al., 2010)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
43	*Hemilepton*	Germany (Wienrich, 1999)			Atlantic	No data	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

44	*Heteranomia*	Belgium (Vandenberghe et al., 2005)	United Kingdom (Woods, 1850); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967); Italy (Bellomo, 1993); Iceland (Eiriksson et al., 2004)	Atlantic	Atlantic	Atlantic
45	*Hiatella*	Germany (*arctica*[a], Wienrich, 1999); Belgium (Vandenberghe et al., 2005); North Pacific (Gladenkov, 1978)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002); Gulf of Alaska (*arctica*[a], MacNeil, 1965); Kamchatka Kafanov, Ogasawara, 2004)	United Kingdom (Norton, 1967); Italy (Bellomo, 1993); Greenland (Simonarson et al., 1998); Alaska (Allison, 1973)	Atlantic	Pacific	Atlantic
46	*Hyalopecten*				No data	No data	Atlantic
47	*Idas*				No data	No data	Atlantic
48	*Katadesmia*				No data	No data	Uncertain
49	*Kellia*	Europe (*suborbicularis*[a], Glibert, Van de Poel, 1967)	United Kingdom (*suborbicularis*[a], Woods, 1850); Belgium (*suborbicularis*[a], Marquet, 1995)	Japan (Itoigawa, Ogawa,1973)	Atlantic	Atlantic	Atlantic
50	*Kelliella*	Parathethys (Studencka et al., 1998)	Italy, France (Janssen, Krylova, 2012)	Italy (Philippi, 1844)	Atlantic	Atlantic	Atlantic
51	*Kurtiella*	Germany (as *Mysella*, Wienrich, 1999)	Belgium (Marquet, 2002)	United Kingdom (Norton, 1967)	Atlantic	Atlantic	Atlantic
52	*Laevicardium*	Italy (Marasti, 1973); Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1879); Belgium (Marquet, 2002); Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (Norton, 1967)	Atlantic	Uncertain	Atlantic
53	*Lampeia*				No data	No data	Pacific
54	*Lasaea*	Poland (Studencka, 1994)	United Kingdom (Wood, 1879)	France (Zibrowius, 1995)	Atlantic	Atlantic	Atlantic
55	*Ledella*	North Sea basin (Wienrich, 1999)			Atlantic	No data	Atlantic
56	*Limaria*	Spain (Jimenez, Braga, 1993); Poland (Studencka, 1994)	United Kingdom (Woods, 1850); Belgium (Marquet, 2002)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

57	*Limatula*	Poland (*subauriaculata*[a]; Studencka, 1994); Hokkaido (Amano, 1986)	United Kingdom (Woods, 1850); Belgium (Marquet, 2002)	Alaska (Allison, 1973)	Atlantic for L. *subau-riculata*[a]; uncertain for others	Atlantic	Atlantic
58	*Limopsis*	Bulgaria (Popov et al., 1996); Germany (*aurita*[a], Wienrich, 1999); Oregon (Moore, 1963)	United Kingdom (Wood, 1850); Spain (*aurita*[a], Lozano Francisco et al., 1993); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967)	Atlantic	Atlantic	Atlantic
59	*Liocyma*	Kamchatka (Kafanov, Ogasawara, 2004)	Kamchatka (Kafanov, Ogasawara, 2004)	Alaska (Allison, 1973)	Pacific	Pacific	Pacific
60	*Lucinoma*	Belgium (*borealis*[a], Vandenberghe et al., 2005); Oregon (Moore, 1963)	United Kingdom (Wood, 1879); Belgium (Marquet, 2002); Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (Norton, 1967); Italy (Bellomo, 1993)	Atlantic	Uncertain	Atlantic
61	*Lutraria*	Italy (Bernasconi, Robba, 1993); Poland (Studencka, 1994)	United Kingdom (Wood, 1850); Belgium (Marquet, 2002); Japan (Hayasaka, 1973)	North Sea Basin (Meijer, 1993)	Atlantic	Uncertain	Atlantic
62	*Lyonsia*	Germany (aff. *norwegica*[a], Wienrich, 1999); Belgium (Vandenberghe et al., 2005); Pribylov Islands (*arenosa*[a], Grant, Gale, 1931); Alaska (Marincovich, 1983);	Iceland (Gladenkov, 1978); Belgium (Marquet, 2002)	North-Western Atlantic (Richards, 1962)	Atlantic for *norwegica*[a]; Pacific for *arenosa*[a]	Atlantic	Atlantic for *L. norwegica*[a]; Pacific for *L. arenosa*[a]
63	*Lyonsiella*				No data	No data	Atlantic
64	*Macoma*	Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (Wood, 1850); Northeast European region of Russia (*balthica*[a], Merklin et al., 1979); Belgium (Marquet, 2002); Kamchatka Kafanov, Ogasawara, 2004);	United Kingdom (Gladenkov, 1978); Northeast European region of Russia (*balthica*[a], *calcarea*, Merklin et al., 1979); Greenland (Simonarson et al., 1998)	Pacific	Uncertain	Pacific
65	*Mactra*	Belgium (Vandenberghe et al., 2005)	United Kingdom (*stultorum*[a], Wood, 1850)	United Kingdom (*stultorum*[a], Gladenkov, 1978)	Atlantic	Atlantic	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

66	*Megayoldia*	Kamchatka (Kafanov et al., 2001)	Western North America (Kafanov et al., 2001)	North Europe (Janssen et al., 2003)	Pacific	Pacific	Pacific
67	*Mendicula*		United Kingdom (Wood, 1850); Belgium (Marquet, 2002)		No data	Atlantic	Atlantic
68	*Mimachlamys*	Greece (Dermitzakis, Georgiades-Dikeoulia, 1987)	Belgium (Marquet, 2002)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
69	*Modiolarca*	Bulgaria (Popov et al., 1996)	Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
70	*Modiolula*	Poland (Studencka, 1994); Germany (*faseolina*[a], Moths et al., 2010)	Belgium (Marquet, 2002)	United Kingdom (Woods, 1850)	Atlantic	Atlantic	Atlantic
71	*Modiolus*	Poland (*adriaticus*[a]; Studencka, 1994); Sakhalin (Kafanov, Ogasawara, 2003); Oregon (Moore, 1963)	Belgium (*modiolus*[a]; Marquet, 2002); Sakhalin (*modiolus*[a]; Kafanov, Ogasawara, 2003);	Iceland (*modiolus*[a]; Gladenkov, 1978); Mediterranean (*modiolus*[a]; Golikov, 1985)	Atlantic for *adriaticus*[a]; Pacific for others	Uncertain for *modiolus*[a]	Atlantic for *M. adriaticus*[a], Pacific for *M. modiolus*[a]
72	*Monia*	Kamchatka (Kafanov, Ogasawara, 2004)	Japan (Hayasaka, 1973)	Alaska (Allison, 1973)	Pacific	Pacific	Pacific
73	*Montacuta*	Poland (Studencka, 1994)	Belgium (Marquet, 2002)	United Kingdom (Woods, 1879)	Atlantic	Atlantic	Atlantic
74	*Musculus*	Paratethys (*discors*[a]; R. Janssen, pers. com.); Poland (*biformis*, Studencka, 1994); Kamchatka (*niger*[a]; Gladenkov, 1978); Alaska (*niger*[a]; Marincovich,1983)	North-Eastern European region of Russia (*niger*[a], Merklin et al., 1979); Greenland (*niger*[a]; Funter et al., 2001); Belgium (*discors*[a]; Marquet, 2005); Kamchatka (*niger*[a], Kafanov, Ogasawara, 2004)	Cumberland (West Atlantic) (*M. glacialis*[a]; Richards, 1962); Iceland (*niger*[a]; Gladenkov, 1978); Chukotka (*discors*[a], *niger*[a]; Merklin et al., 1962)	Atlantic for *discors*[a]; Pacific for *niger*[a]; uncertain for *glacialis*[a], *laevigatus*[a]	Atlantic for *discors*[a]; Pacific for *niger*[a]; uncertain for *glacialis*[a], *laevigatus*[a]	Atlantic for *M. discors*[a]; Pacific for *M. niger*[a]; uncertain for *M. glacialis*[a], *M. laevigatus*[a]
75	*Mya*	Western North America (MacNeil, 1965); Kamchatka (Gladenkov, 1978); Alaska (Marincovich, 1983)	Iceland (Gladenkov, 1978); Western North America (MacNeil, 1965); Kamchatka Kafanov, Ogasawara, 2004)	United Kingdom (Gladenkov, 1978); Northeast European region of Russia (*pseudo-arenaria*[a], *truncata*[a], Merklin et al., 1979); Poland (Makowska, 1986); Alaska (Allison, 1973);	Pacific	Pacific	Pacific
76	*Myonera*				No data	No data	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

77	*Myrtea*	Italy (Bernasconi, Robba, 1993); Bulgaria (Popov et al., 1996)			Atlantic	No data	Atlantic
78	*Mysella*				No data	No data	Pacific
79	*Mysia*				No data	No data	Atlantic
80	*Mytilus*	France (close to *galloprovincialis,* Kafanov, 1987); Oregon (Moore, 1963); West Kamchatka (close to *edulis*[a], Gladenkov, 1978; Kafanov,1987);	Northeast European region of Russia (*edulis*[a], Merklin et al., 1979); United Kingdom, Iceland (*edulis*[a], Gladenkov, 1978); Greenland (Funter et al., 2001); Belgium (*edulis*[a], Marquet, 2002); Kamchatka (Kafanov, Ogasawara, 2004)	Iceland (Gladenkov, 1978); Northeast European region of Russia (*edulis*[a], Merklin et al., 1979); Greenland (Simonarson et al., 1998); Italy (Bellomo, 1993); Chukotka (Merklin et al., 1962)	Pacific for *edulis*[a]	Uncertain	Pacific
81	*Notolimea*				No data	No data	Atlantic
82	*Nototeredo*		United Kingdom (Wood, 1850)	France (as *Teredo norvagica*[a], de Lumley, 1988)	No data	Atlantic	Atlantic
83	*Nucula*	Paratethys (Studencka et al., 1998); Germany (Wienrich, 1999)	United Kingdom (Woods, 1850); Greenland (Funder et al., 2001)	Greenland (Simonarson et al., 1998); Italy (Ragaini et al., 2007)	Atlantic	Atlantic	Atlantic
84	*Nuculana*	North Alaska, Kamchatka (Kafanov, Ogasawara, 2004)	Iceland (Gladenkov, 1978); Northeast European region of Russia (*pernula*[a], Merklin et al., 1979); Japan (Amano et al., 2000)	North-Western Atlantic (Richards, 1962); Northeast European region of Russia (*pernula*[a], Merklin et al., 1979)	Pacific	Pacific	Pacific
85	*Ostrea*	Germany (Wienrich, 1999)	United Kingdom (Woods, 1850)	Italy (Bellomo, 1973)	Atlantic	Atlantic	Atlantic
86	*Palliolum*	Poland (Studencka, 1994)	United Kingdom (Woods, 1850); Belgium (Marquet, 2005)	United Kingdom (Norton, 1967)	Atlantic	Atlantic	Atlantic
87	*Pandora (Pandorella)*	Japan (Takayasu, 1986); Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (Wood, 1879); Virginia (*arenosa*; Ward, 1993); Belgium (Marquet, 2002); Kamchatka (Kafanov, Ogasawara, 2004)	Northwest Atlantic (*glacialis*[a], Richards, 1962); Greenland (Simonarson et al., 1998)	Pacific	Uncertain	Pacific

Table 3 (continuing)
Таблица 3 (продолжение)

88	*Panomya*	Kamchatka (Kafanov, Ogasawara, 2004); Hokkaido (Nakashima, 2005)	Iceland (Gladenkov, 1978); Kamchatka (Kafanov, Ogasawara, 2004); Hokkaido (Nakashima, 2005)	Barents Sea (Merklin et al., 1979); Poland (Makowska, 1986); Alaska (Allison, 1973); Hokkaido (Nakashima, 2005)	Pacific	Pacific	Pacific
89	*Parilimya*				No data	No data	Atlantic
90	*Parvicardium*	Belgium (Vandenberghe et al., 2005)	Belgium (Marquet, 2002)	Turkey (Schneideret al., 2005)	Atlantic	Atlantic	Atlantic
91	*Pecten*	North Europe (Gladenkov, 1978)	United Kingdom (Wood, 1879); Italy (Dieni, Omenetto, 1960)	Spain (Vera-Peláez et al., 2004)	Atlantic	Atlantic	Atlantic
92	*Periploma* (*Septentrioploma*)	Alaska (*aleutica*[a], Marincovich, 1983)	Arctic Alaska (MacNeil, 1957)		Pacific	Uncertain	Pacific
93	*Peronidia*	Alaska (Marincovich, 1983)	California (Addicott, 1969)		Pacific	Pacific	Pacific
94	*Pharax*				No data	No data	Atlantic
95	*Pholas*		United Kingdom (Wood, 1879)		No data	Atlantic	Atlantic
96	*Pododesmus*	Poland (Studencka, 1994)	United Kingdom (Woods, 1850); Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
97	*Policordia s.s.*				No data	No data	Atlantic
98	*Poromya*	Cyprus (Reed, 1935)	United Kingdom (Wood, 1879); Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
99	*Portlandia*	Japan (Honda, 1989)	Greenland (Funder et al., 2001); Japan (Honda, 1989)	Iceland (Gladenkov, 1978); Greenland, (Símonarsson et al., 1998); Italy (Ragaini et al., 2007); Canada: Ontario, Quebec (Wagner, 1970); Kamchatka (Gladenkov, 1978); Japan (Okamoto, Ibaraki, 1988)	Pacific	Pacific	Pacific
100	*Pseudamussium*	Paratethys (Gontsharova, 1989)	Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
101	*Pseudomalletia*				No data	No data	Atlantic
102	*Pseudoneilonella*				No data	No data	Atlantic
103	*Pseudopythina*				No data	No data	Pacific
104	*Psiloteredo*	Europe (Janssen, 1972)			Atlantic	No data	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

105	*Rochefortia*			Alaska (Allison, 1973)	No data	No data	Pacific
106	*Ruditapes*		Sakhalin (Kafanov, Ogasawara, 2003)	Japan (Okamoto, Ibaraki, 1988)	No data	Pacific	Atlantic
107	*Saxicavella*	Germany (Wienrich, 1999)			Atlantic	No data	Atlantic
108	*Scrobicularia*		Italy (Benvenuti, Dominici, 1992)	Poland (Makowska. 1986)	No data	Atlantic	Atlantic
109	*Serripes*	Japan (Takayasu, 1986); Sakhalin (Kafanov, Ogasawara, 2003)	United Kingdom (Woods, 1850); Northeast European region of Russia (*groenlandicus*[a], Merklin et al., 1979); Iceland (Buchardt, Simonarson, 2003); Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (Norton, 1967); Northeast European region of Russia (*groenlandicus*[a], Merklin et al., 1979); Greenland (Simonarson et al., 1998); Alaska (Allison, 1973)	Pacific	Pacific	Pacific
110	*Sphenia*	Poland (Studencka, 1994)	Belgium (Marquet, 2002)	North Carolina (Miller, 1990)	Atlantic	Atlantic	Atlantic
111	*Siliqua*	Alaska (Marincovich, 1983)	Kamchatka (Kafanov, Ogasawara, 2004)	Oregon (Arnold, Hannibal, 1913)	Pacific	Pacific	Pacific
112	*Similipecten*	Belgium (Vandenberghe et al., 2005)	United Kindom (Wood, 1879); Iceland (Gladenkov, 1978); Northeast European region of Russia (*greenlandicus*[a], Merklin et al., 1979); Belgium (Marquet, 2002)	Northwest Atlantic (Richards, 1962); Northeast European region of Russia (*greenlandicus*[a], Merklin et al., 1979); Greenland (Bennike et al., 1994)	Atlantic	Atlantic	Atlantic
113	*Spisula* (*Spisula*)	Poland (Studencka, 1994); Germany (*elliptica*[a], Wienrich, 1999); Belgium (Vandenberghe et al., 2005)	United Kingdom (Wood, 1850); Italy (Benvenuti, Dominici, 1992); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967); Northeast European region of Russia (*elliptica*[a], Merklin et al., 1979); Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
114	*Syssitomya*				No data	No data	Atlantic
115	*Talochlamys*	Spain (Mankiewicz, 1996)	United Kingdom (Woods, 1850)		Atlantic	Atlantic	Atlantic
116	*Tapes* (*Tapes*)	Bulgaria (Popov et al., 1996)	United Kingdom, Iceland (Gladenkov, 1978)	Iceland (Gladenkov, 1978)	Atlantic	Atlantic	Atlantic
117	*Tellina*	Poland (Studencka, 1994)	United Kingdom (Gladenkov, 1978)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic

Table 3 (continuing)
Таблица 3 (продолжение)

118	*Tellimya*		United Kingdom (Woods, 1850); Belgium (Marquet, 2002)	United Kingdom (Norton, 1967)		Atlantic	Atlantic
119	*Teredo*	Europe (Janssen, 1972)	United Kingdom (Wood, 1850)	Spain (Corchón et al., 2008)	Atlantic	Atlantic	Atlantic
120	*Thracia* s.l.	Italy (*convexa*[a], Marasti, 1973); Poland (Studencka, 1994); Belgium (Vandenberghe et al., 2005); Alaska (as *Thracia* sp., Marincovich, 1983)	United Kingdom (*phaseolina*[a], Wood, 1879); Arctic Alaska (*septentrionalis*[a], MacNeil, 1957); Belgium (*convexa*[a], Marquet, 2002)	Northwest Atlantic (*septentrionalis*[a], Richards, 1962)	Atlantic	Atlantic	Atlantic
121	*Thyasira*	Poland (*flexuosa*[a], Studencka, 1994); Arctic Alaska (*arctica*[a], MacNeil, 1957); Kamchatka (*nana*, Kafanov, Ogasawara, 2003)	Belgium (*flexuosa*[a], Marquet, 2002); Kamchatka (*cf. gouldii*[a], Kafanov, Ogasawara, 2004)	Greenland (*gouldii*[a], Simonarson et al., 1998); Iceland (Eiriksson et al., 2004)	Atlantic	Atlantic for *flexuosa*[a]; Pacific for *gouldii*[a]	Atlantic
122	*Timoclea*	Poland (Studencka, 1994)	Belgium (Marquet, 2002)	United Kingdom (Norton, 1967); Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
123	*Tindaria*				No data	No data	Atlantic
124	*Tropidomya*				No data	No data	Atlantic
125	*Turtonia*			Alaska (Allison, 1973)	No data	No data	Uncertain
126	*Varicorbula*	Poland (Studencka, 1994); Belgium (Vandenberghe et al., 2005)	Italy (Benvenuti, Dominici, 1992); Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
127	*Venerupis*		United Kingdom (Gladenkov, 1978); Iceland (Norton, 1975)		No data	Atlantic	Atlantic
128	*Venus*	Poland (Studencka, 1994)	United Kingdom (Wood, 1879)	Italy (Bellomo, 1993)	Atlantic	Atlantic	Atlantic
129	*Xylophaga*	Germany (Wienrich, 1999)	Belgium (Marquet, 2002)		Atlantic	Atlantic	Atlantic
130	*Yoldia*	Belgium (Vandenberghe et al., 2005); Kamchatka, Sakhalin (*hyperborea*[a], Kafanov, Ogasawa, 2004)	United Kingdom, Nederland (Gladenkov, 1978); Kamchatka (Kafanov, Ogasawara, 2004)	Greenland (Bennike et al., 2004); Chukotka (Merklin et al, 1962)	Pacific for *hyperborea*[a]	Uncertain	Pacific

Table 3 (continuing)
Таблица 3 (продолжение)

131	*Yoldiella*	Belgium (Vandenberghe et al., 2005)	Northeast European region of Russia (*lenticula*[a], Merklin et al., 1979); Northwest Atlantic (Gladenkov, 1978); Iceland (Gladenkov, 1978); Greenland (*intermedia*[a], Simonarson et al., 1998)	Northwest Atlantic (Richards, 1962); Northeast European region of Russia (*lenticula*[a], Merklin et al., 1979); Norwegian Sea (Thomsen, Vorren, 1986); Greenland (*intermedia*[a], Simonarson et al., 1998); Chukotka (Svitoch, 2003)	Atlantic	Atlantic	Atlantic
132	*Zirfaea*	Kamchatka (Kafanov, Ogasawara, 2004)	United Kingdom (*crispata*[a], Wood, 1879); Belgium (Marquet, 2002)	Northwest Atlantic (*crispata*[a], Richards, 1962); Iceland (Eiriksson et al., 2004	Pacific	Atlantic	Pacific

[a] – species currently occurring in the Arctic Ocean

genera in which part of modern Arctic species occur in fossils in the North Atlantic and part in the North Pacific in Late Miocene-Early Pliocene.

The identification of a region, from which penetration into the Arctic took place, by data on the modern distribution of species, was based on a complex of characters of approximately equal importance.

The following distribution patterns were considered as evidence for a higher probability of Pacific origin:

1. A genus is known from the North Pacific and not recorded from the North Atlantic.

2. The number of species is higher in the North Pacific than in the North Atlantic.

3. Arctic species occur also in the North Pacific but are not recorded from the North Atlantic.

4. Arctic species have a near-Pacific distribution.

Analogous criteria were used to assign the origin of species to the Atlantic. Genera were identified as of uncertain origin when evidences for the Pacific and the Atlantic origin were similar. For example, a genus could be represented by more species in the North Pacific, but Arctic species are known from the North Atlantic. Genera were considered to be autochthonous if they are not known outside the Arctic Ocean. These criteria do not allow the determination of the dual colonization of a genus. However, in some cases, for example when there are Arctic species of a genus occurring in the Atlantic and not known in the Pacific, and there are Arctic species occurring in the Pacific but not known in the Atlantic, we suggest independent colonization.

A second analysis was based on the modern distribution of species, in which the presence of species common with the North Pacific was regarded as more important evidence than that with the North Atlantic. So the Pacific origin was adopted for some genera in which the number of North Atlantic species is the same or even higher than North Pacific species (Table 4).

This analysis considers the fact that the probability of penetration of Atlantic species into the North Pacific through the Arctic is less than probability of penetration of species from the North Pacific into the North Atlantic, as evidenced by both paleodata and molecular analysis (Durham, MacNeil, 1967; Vermeij, 1991; Dodson et al., 2007). As s result of both analyses based on the modern distribution of species, we obtained two numbers for genera of supposedly Pacific origin: the first most likely underestimating, the second overestimating the “real” number.

The final conclusion, about the probable region of penetration into the Arctic, was made based on combined data: paleo-records and the pattern of current distribution. Paleo-data was given a higher ranking than the modern distribution. A few available molecular data (for the genera *Arctica*, *Chlamys*, *Macoma*, *Modiolus* and *Mytilus*) were used in the analysis (Dahlgren et al., 2000; Galand, Fevolden, 2000; Väinölä, 2003; Nikula et al., 2007; Lockwood et al., 2010).

Results

Ratio of species in different Arctic regions common with the North Pacific and the North Atlantic

Shallow-water regions

The number of bivalve species in marginal Eurasian seas (depth up to 300 m) diminishes from the Norwegian Sea (193 spp.) towards the East Siberian Sea (59 spp.) and then increases in the Chukchi Sea (72 spp.) (Figs 1, 2) before decreasing in the Beaufort Sea (61 spp.) (Table 2). The most drastic changes in species numbers occur at the transition from the Norwegian Sea to the Barents Sea (a nearly a twofold decrease) and from the Barents Sea to the Kara Sea (a 1.5 times decrease). The share of species in common with the Atlantic decreases from the Norwegian to the Chukchi Sea, then it slightly increases in the Beaufort Sea. The trends of changes in the share of species common with the Atlantic and the total species number coincide: the most significant changes occur at the transition from the Norwegian Sea to the Barents Sea and from the latter to the Kara Sea. The share of species common with the Pacific gradually increases from the Norwegian Sea to the Chukchi Sea, and then decreases in the Beaufort Sea. The most drastic change occurs in transition from the East Siberian Sea to the Chukchi Sea, where the share of species common with the Pacific increases more than twofold. The prevailing share of species common with the Atlantic characterizes the majority of shallow-water regions of the Arctic. The exceptions are the Chukchi and Beaufort seas. The share of species common with both the Atlantic and the Pacific increases from the Norwegian Sea, reaching a maximum in the East Siberian and Beaufort seas. All shallow-water regions, except for the Norwegian Sea, are mainly inhabited by species common to both the Atlantic and the Pacific.

Deep-sea regions

Deep-sea basins are inhabited by far fewer bivalve species than the shallow-water regions (Fig. 1, 2; Table 2). Deep-sea basins are characterized by the absence, or very small share of, species known only from the Pacific. The Arctic deep-sea basins mainly contain species known either only from the Atlantic (Nansen and Amundsen Basins), or from the Atlantic and also common to both the Atlantic and the Pacific (Norwegian and Greenland Basins), or are Arctic endemics (Canada Basin).

Origin of genera

Paleontological approach

Paleo-data was available for 111 genera of Arctic bivalves, but three genera were recorded only from Pleistocene and that is not enough to make conclusions regarding the area of origin. Therefore the paleo-data allowed speculation about origin of 108 genera. Based on paleo-records from Middle Miocene deposits, the area of origin was suggested for 97 genera (72% of all Arctic genera) (Figs 6A, 7A). Colonization from the North Atlantic is suggested for 71 genera and from the North Pacific for 23 genera with independent colonization from both regions for three genera (Table 3). Paleo-records dating to the Pliocene were used to reconstruct the area of origin for 99 genera (74%). Colonization from the North Atlantic is suggested for 70 genera and from the North Pacific for 17 genera. Independent colonization from both regions is suggested for two genera. The area of origin remains uncertain for 10 genera (Table 3).

The large number of genera of uncertain origin in the second version of the analysis can be related to insufficient resolution of the method (too long time periods). For example, if over the entire Pliocene there were records of a genus in both the North Pacific and the Atlantic, the area of the genus origin was considered uncertain. Perhaps the use of the Pliocene subdivisions could help in clarification of the time at which the genus appeared in different regions. The number of genera of the Atlantic origin differs insignificantly between both versions of the analysis.

Neontological approach

Conclusions about the origin of all 132 genera were based on the four biogeographic criteria presented earlier (Table 4) (Figs 6B, 7B). Based on the first criterion (when a genus is absent in the northern part of one ocean but present in the Arctic and in the north of the other ocean), the region of penetration into the Arctic was identified for 61 genera. The origin of the remaining 72 genera was established in two versions based on the combination of criteria 2–4.

According to the first analysis, with all criteria of equal weight, 98 genera were of Atlantic origin, 21 genera of Pacific origin, one genus was autochthonous and 12 genera were of uncertain origin. In the second analysis, when the Atlantic-Arctic species ranges were considered less important than the Pacific-Arctic species ranges, the ratio between genera of different origin has changed. The group of the Atlantic origin decreased by 12 genera while the group of Pacific origin increased by 15 genera and the group of uncertain origin decreased by 6 genera (Table 4).

Despite the increased number of genera of the Pacific origin in the second analysis, this number was still much lower than the number of genera of the Atlantic origin. The results for 114 genera (86% of the Arctic genera) were the same in both versions.

Comparison of results of paleontological and neontological approaches

The region of penetration into the Arctic was proposed based on both paleontological and neontological data for 104 genera. The results

Table 4. Distribution of recent Arctic genera and their inferred ocean of origin, based on recent distributions. Abbreviations: A — species with Arctic-Atlantic ranges; AN — species known in the Arctic only from the Norwegian Sea; AP — species with Arctic-Atlantic-Pacific ranges; P — species with Arctic-Pacific ranges; E — Arctic endemic species.

Таблица 4. Распространение родов современных арктических двустворчатых моллюсков и предполагаемый район проникновения в Арктику; вывод о районе проникновения сделан на основе современного распространения.

Обозначения: A — виды известные из Арктики и Атлантики; AN — виды известные в Арктике только из Норвежского моря; AP — виды известные из Арктики, Атлантики и Пацифики, P — виды известные из Арктики и Пацифики; E — эндемики Арктики.

	Genus	Number of species				Region of penetration into the Arctic, based on recent distributions	
		Approximate total number	Arctic	Northern Atlantic	Northern Pacific	I^st version	II^nd version (if different from the I^st version)
1	*Abra*	49	5AN	7	2	Atlantic	
2	*Acanthocardia*	6	1A	6	0	Atlantic	
3	*Acesta*	29	1AN	1	1	Atlantic	
4	*Aequipecten*	9	1AN	2	0	Atlantic	
5	*Altenaeum*	1	1AP	1	1	Uncertain	Pacific
6	*Arca*	21	1AN	2	1	Atlantic	
7	*Arcopagia*	5	1AN	2	0	Atlantic	
8	*Arctica*	1	1A	1	0	Atlantic	
9	*Asperarca*	6	1AN	3	0	Atlantic	
10	*Astarte s.l.*	46	3A+4AP+6E +3P	21	11	Atlantic	Atlantic-Pacific
11	*Axinopsida*	4	1AP	1	3	Pacific	
12	*Axinulus*	8	1A+1E	3	0	Atlantic	
13	*Barnea* (*Barnea*)	1	1AN	1	0	Atlantic	
14	*Bathyarca*	27	3A	7	1	Atlantic	
15	*Boreacola*	1	1E	0	0	*	
16	*Cardiomya*	55	1AN	9	8	Atlantic	
17	*Cerastoderma*	3	2AN	3	0	Atlantic	
18	*Cetomya*	20	1E	2	1	Uncertain	
19	*Chamelea*	2	1AN	2	0	Atlantic	
20	*Chlamys*	15	1A+2P	1	7	Pacific	
21	*Ciliatocardium*	2	1AP	1	2	Pacific	
22	*Clausinella*	4	1AN	2	0	Atlantic	

Table 4 (continuing)
Таблица 4 (продолжение)

23	*Cochlodesma*	6	1AN	2	0	Atlantic	
24	*Crenella*	15	1A+1AP	7	1	Atlantic	
25	*Cuspidaria*	120	4A+1AN+2AP+1E	21	7	Atlantic	Pacific
26	*Cyclocardia*	22	3P	2	9	Pacific	
27	*Cyclopecten*	47	1A	12	8	Atlantic	
28	*Cyrtodaria*	2	1AP	2	1	Atlantic	Pacific
29	*Dacrydium*	29	1A+1AP	6	3	Atlantic	Pacific
30	*Delectopecten*	9	1A	1	2	Uncertain	
31	*Devonia*	1	1AN	1	0	Atlantic	
32	*Diplodonta*	22	1P+1A	7	2	Atlantic	Atlantic-Pacific
33	*Dosinia* s.l.	103	2AN	4	4	Atlantic	Uncertain
34	*Ennucula*	47	1A+1AP +1E	4	3	Atlantic	Pacific
35	*Ensis*	12	4AN	5	0	Atlantic	
36	*Epilepton*	2	2AN	2	0	Atlantic	
37	*Gari*	64	3AN	6	1	Atlantic	
38	*Glossus*	1	1AN	1	0	Atlantic	
39	*Glycymeris (Glycymeris)*	28	1AN	6	0	Atlantic	
40	*Goethemia*	1	1AN	1	0	Atlantic	
41	*Goodallia*	5	1AN	5	0	Atlantic	
42	*Gouldia*	4	1AN	1	0	Atlantic	
43	*Hemilepton*	1	1AN	1	0	Atlantic	
44	*Heteranomia*	1	1A	1	0	Atlantic	
45	*Hiatella*	4	1A +1AP	2	1	Atlantic	Pacific
46	*Hyalopecten*	10	1A	2	0	Atlantic	
47	*Idas*	12	1AN	5	2	Atlantic	
48	*Katadesmia*	7	1E	1	1	Uncertain	
49	*Kellia*	8	1AP	1	4	Pacific	
50	*Kelliella*	3	1A	1	0	Atlantic	
51	*Kurtiella*	15	2AN	5	0	Atlantic	
52	*Laevicardium*	15	1AN	4	0	Atlantic	
53	*Lampeia*	3	1P	0	3	Pacific	
54	*Lasaea*	3	1AN	1	0	Atlantic	

Table 4 (continuing)
Таблица 4 (продолжение)

55	*Ledella*	46	1AN	7	2	Atlantic	
56	*Limaria*	48	2AN	3	0	Atlantic	
57	*Limatula*	70	3A+1AP	12	4	Atlantic	
58	*Limopsis*	22	2A	8	3	Atlantic	
59	*Liocyma*	1	1AP	1	1	Uncertain	Pacific
60	*Lucinoma*	28	1A	5	2	Atlantic	
61	*Lutraria*	19	1AN	3	0	Atlantic	
62	*Lyonsia*	21	1A+1AP	5	6	Uncertain	Pacific
63	*Lyonsiella*	21	1A	6	1	Atlantic	
64	*Macoma*	49	2AP+6P	4	14	Pacific	
65	*Mactra*	70	1AN	4	2	Atlantic	
66	*Megayoldia*	6	1AP	1	3	Pacific	
67	*Mendicula*	9	1A+1AP	3	1	Atlantic	Pacific
68	*Mimachlamys*	11	1AN	1	0	Atlantic	
69	*Modiolarca*	1	1AN	1	0	Atlantic	
70	*Modiolula*	1	1AN	1	0	Atlantic	
71	*Modiolus*	36	1A+1AP	8	3	Atlantic	Pacific
72	*Monia*	6	1P	0	1	Pacific	
73	*Montacuta*	15	1A+1AN+1AP	10	1	Atlantic	
74	*Musculus*	12	4AP	5	5	Uncertain	
75	*Mya*	8	2AP+2E +2P	2	6	Pacific	
76	*Myonera*	19	1E	4	2	Atlantic	
77	*Myrtea*	20	1AN	2	0	Atlantic	
78	*Mysella*	15	3P	4	4	Pacific	
79	*Mysia*	3	1AN	1	0	Atlantic	
80	*Mytilus*	10	1A+1AP	3	3	Uncertain	Pacific
81	*Notolimea*	3	1AN	2	0	Atlantic	
82	*Nototeredo*	4	1A	1	0	Atlantic	
83	*Nucula*	97	5A+1E	9	2	Atlantic	
84	*Nuculana*	127	2AP+1P	6	6	Pacific	
85	*Ostrea*	38	1AN	1	0	Atlantic	
86	*Palliolum*	4	2A+1AN	3	0	Atlantic	

Table 4 (continuing)
Таблица 4 (продолжение)

87	*Pandora* (*Pandorella*)	35	1AP	3	2	Uncertain	Pacific
88	*Panomya*	6	1AP+2P	1	6	Pacific	
89	*Parilimya*	9	1AN	2	2	Atlantic	
90	*Parvicardium*	10	4AN	10	0	Atlantic	
91	*Pecten*	27	1AN	2	1	Atlantic	
92	*Periploma* (*Septentrioploma*)	4	1AP	2	3	Pacific	
93	*Peronidia*	4	1P	1	3	Pacific	
94	*Pharax*	3	1AN	2	0	Atlantic	
95	*Pholas*	5	1AN	1	0	Atlantic	
96	*Pododesmus*	7	1A	4	0	Atlantic	
97	*Policordia* s.str.	25	1A+1E	5	1	Atlantic	
98	*Poromya*	24	1A	1	1	Uncertain	
99	*Portlandia*	6	1AP+1P+1E	1	2	Pacific	
100	*Pseudamussium*	6	1A+1AN	5	0	Atlantic	
101	*Pseudomalletia*	3	1AN	1	0	Atlantic	
102	*Pseudoneilonella*	1	1AN	1	0	Atlantic	
103	*Pseudopythina*	2	1P	0	1	Pacific	
104	*Psiloteredo*	3	1A	1	0	Atlantic	
105	*Rochefortia*	6	1P	0	3	Pacific	
106	*Ruditapes*	3	1AN	1	1	Atlantic	
107	*Saxicavella*	5	1A	2	0	Atlantic	
108	*Scrobicularia*	3	1AN	2	0	Atlantic	
109	*Serripes*	3	1AP+1P	1	3	Pacific	
110	*Sphenia*	12	1AN	3	1	Atlantic	
111	*Siliqua*	12	1P	2	2	Pacific	
112	*Similipecten*	7	2A	3	0	Atlantic	
113	*Spisula* (*Spisula*)	14	1A + 1AN	4	0	Atlantic	
114	*Syssitomya*	1	1A	1	0	Atlantic	
115	*Talochlamys*	12	1AN	2	0	Atlantic	
116	*Tapes* (*Tapes*)	2	2AN	2	0	Atlantic	

Table 4 (continuing)
Таблица 4 (продолжение)

117	*Tellina*	87	3AN	13	1	Atlantic	
118	*Tellimya*	11	2AN	2	0	Atlantic	
119	*Teredo*	12	1AN	2	2 (recently introduced)	Atlantic	
120	*Thracia* s.l.	47	5A+3AP	11	6	Atlantic	Pacific
121	*Thyasira*	46	5A+2AP+1P	28	4	Atlantic	Pacific
122	*Timoclea*	27	1A	2	0	Atlantic	
123	*Tindaria*	28	1E	4	2	Atlantic	
124	*Tropidomya*	2	1AN	1	0	Atlantic	
125	*Turtonia*	1	1AP	1	1	Uncertain	Pacific
126	*Varicorbula*	8	1AN	1	0	Atlantic	
127	*Venerupis*	16	1AN	5	0	Atlantic	
128	*Venus*	18	1AN	3	0	Atlantic	
129	*Xylophaga*	42	1A+3AN	10	5	Atlantic	
130	*Yoldia*	15	3AP+1P	5	7	Pacific	
131	*Yoldiella*	42	8A+3AP+2E	28	5	Atlantic	
132	*Zirfaea*	2	1AN+1P	1	1	Uncertain	Atlantic-Pacific

* considered to be an autochthonous genus

of the two approaches disagreed for 15 genera. The following are several examples where results of neontological and paleontological approaches diverge.

The genus *Ennucula* according to the formal criterion of the first version of neontological analysis, is of Atlantic origin (Table 4). Since the number of species of this genus occurring in the North Atlantic (four) and the North Pacific (three) differ insignificantly, we consider the ranges of the Arctic species. There are three species of *Ennucula* in the Arctic. One Arctic species, *E. corticata* (Møller, 1842), occurs in the near-Atlantic part of the Arctic but not further than the Barents Sea. The second species, *E. tenuis* (Montagu, 1808), is distributed in both the Atlantic and the Pacific, and the third species, *E. romboides* (Scarlato, 1981) is an endemic of the Asian Arctic seas. However, in the paleontological records this genus is known from the northern Pacific, Alaska (Merklin et al., 1962) and Oregon (Moore, 1963) since the Middle Miocene. European Miocene deposits lack this genus and, since the Late Pliocene, it appears in Greenland (Funder et al., 2001) and in the Plio-Pleistocene in Iceland (Gladenkov, 1978) (Table 3). Therefore, we suggest that the genus *Ennucula* colonized the Arctic seas from the Pacific, and the species *E. corticata* and *E. romboides* apparently are so-called derived species (Vermeij, 1991), i.e. they have formed after the penetration of the genus into the Arctic.

There is only one Arctic species of *Ruditapes*, *R. decussatus* (L., 1758). Its range in the Arctic is limited to the Norwegian Sea. In the Atlantic the genus extends to the tropics. Based on the modern distribution of the genus, we suggest that *R. decussatus* colonized the Arctic from the Atlantic. However, the paleo-data do not confirm this: the genus has not been recorded in European deposits. The earliest finding of the genus, is in the Early Pliocene of Sakhalin (Kafanov, Ogasawara, 2003). In the Pleistocene, the genus was recorded in Japan (Okamoto, Ibaraki, 1988). Since the genus is mostly subtropical, we suggest that it penetrated the Atlantic from the North Pacific, having spread along the low latitudes. Eventually, this genus colonized the Arctic from the Atlantic.

Another genus, *Modiolus*, has two Arctic species, both distributed also in the Atlantic. One species, *M. adriaticus*, does not occur in the Arctic beyond the Norwegian Sea and is not known from the Pacific. The other species, *M. modiolus*, occurs in the Norwegian, White and Barents Seas and is known from the Bering Sea. Based on neontological criteria, the genus has penetrated the Arctic from the Atlantic, because there are eight species of this genus in the North Atlantic and only three in the North Pacific. In fossils, the genus is known from the Middle and Late Miocene of Europe (*M. adriaticus*, Studencka, 1994) as well as Sakhalin (Kafanov, Ogasawara, 2003). Thus, we can only suggest the dual colonization of the Arctic: *M. adriaticus* has Atlantic roots whereas *M. modiolus* is of the Pacific origin. This “dual-origin” colonization pattern is suggested also for *Musculus* and *Lyonsia*.

Based on the modern distribution, it is impossible to establish the region of the Arctic penetration for the genus *Mytilus*, with two Arctic species, *M. edulis* and *M. trossulus*. Paleontological data indicate most likely the Pacific roots for *Mytilus*. Species similar to *M. edulis* have been recorded in the North-West Pacific since the Early Pliocene (Kafanov, 1987). In the North Atlantic, *M. edulis* has been recorded since the Early Pliocene in deposits from the United Kingdom, Iceland and Belgium (Durham, MacNeil, 1967; Gladenkov, 1978). There are numerous reconstructions of the biogeographic history of the genus *Mytilus* based on molecular data, allozyme studies and radiocarbon dates of shells (Varvio et al., 1988; Hansen et al., 2011; Väinölä, Strelkov, 2011). These data suggest that *Mytilus* migrated from the Pacific to the Atlantic at least twice (Varvio et al., 1988). In the first stage, the Pacific species penetrated the Arctic in the Pliocene. Then, after cooling, colonization pathways closed and the Atlantic and Pacific populations diverged and gave origin to the two species, *M. edulis* and *M. trossulus*, respectively. Isolation of the Mediterranean population of *M. edulis* has subsequently led to the origin of *M. galloprovincialis* (Varvio et al., 1988). At the second stage, in the Late Pleistocene or in the Holocene the Pacific species *M. trossulus* migrated again to the Atlantic through the Arctic.

The comparison of neontological and paleontological results shows that the most efficient criterion in the neontological analysis is the

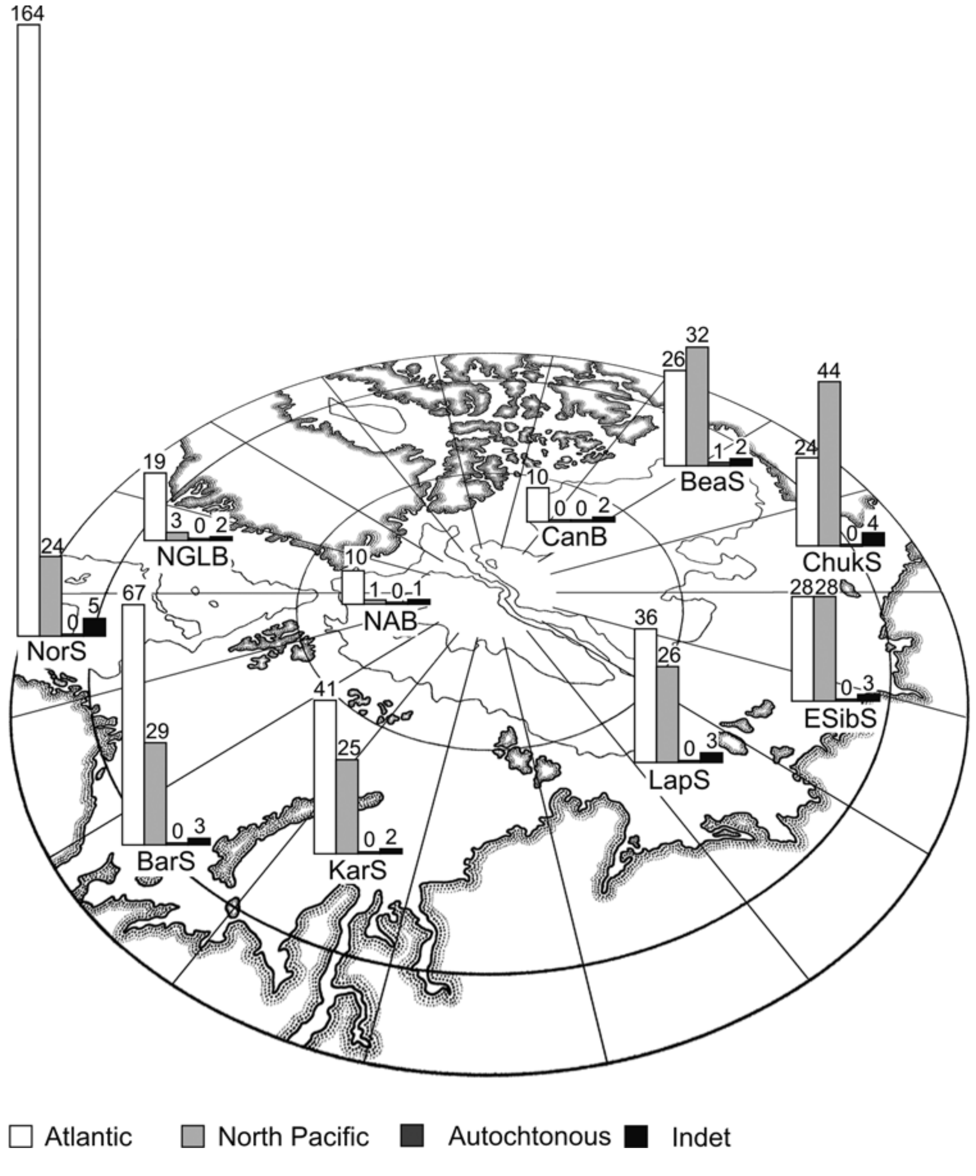


Fig. 3. Number of species of Bivalvia of different origin in various Arctic regions.
Abbreviations: see Fig. 1.
Рис. 3. Число видов двустворчатых моллюсков различного происхождения в разных регионах Арктики.
Обозначения те же, что на Рис. 1.

absence of a genus in the near-Arctic region of one ocean and its presence in the Arctic and near-Arctic area of another ocean. Conclusions based on this criterion corresponded to paleo-data in all cases. Based on the criterion of the presence of a genus in the northern regions of both oceans, but with more species in one region than in the other, our conclusions agreed with paleo-data in 94% of cases. Good correspondence of results supports the choice of criteria for the identification of the area of origin based on the modern distribution. This allowed inclusion, into final analysis, of genera without paleontological records.

In total, among 132 genera, 97 are supposedly of Atlantic origin, 26 of Pacific origin. Three genera are of "dual-origin" and one genus is of autochthonous origin. The origin remains uncertain for five genera (Table 3).

Endemics of the Arctic

Twenty species of bivalves (8% of the total number) are endemic to the Arctic among the species considered. In shallow-water areas, the share of endemics varies from 0 in the Norwegian Sea to 5% in the Laptev Sea. In deep-water basins the percentage of endemics is higher: 13% in the Norwegian and Greenland basins, 33% — in the Nansen and Amundsen basins and 50% in the Canada Basin (Figs 1, 2). Among endemic species, 14 belong to genera of Atlantic origin (*Nucula zophos*, *Tindaria derjugini*, *Yoldiella frami*, *Y. tamara*, *Astarte nuuki*, *A. moerchi*, *A. elonga*, *A. neocrassa*, *A. vaigati*, *A. warhami*, *Axinulus careyi*, *Policordia ushakovi*, *Myonera centobi*, *Cuspidaria turgida*), three belong to genera of Pacific origin (*Ennucula romboides*, *Mya neouddevallensis*, *M. neoovata*), two species belong to genera of uncertain origin (*Katadesmia kolthoffi*, *Cetomya* sp.) and one species belongs to the autochthonous genus (*Boreacola vadosus*). All endemics of Pacific origin are sublittoral, whereas all endemics of the Atlantic origin, except for the species of *Astarte,* are the deep-sea species and nearly all occur in the central basins. In the genus *Astarte* the number of endemic species is exceptionally high: 6. These species, until recently, have been considered as morphological variations of three widely-spread species (*borealis*, *elliptica* and *montagui*). They received a species rank in the work of Petersen (2001). The autochthonous genus *Boreacola* is monotypical.

Distribution of species of different origin in Arctic regions

According to our data, species of genera of Atlantic origin prevail in both the shelf and the deep-sea regions of the Arctic. The share of species of Atlantic origin decreases in marginal Eurasian seas from the Norwegian Sea to the Chukchi Sea and then it somewhat increases in the Beaufort Sea (Figs 3, 4). The share of species of the Atlantic origin decreases most sharply at the transition from the Norwegian Sea to the Barents Sea and from the East Siberian Sea to the Chukchi Sea. The share of species of Pacific origin increases from the Norwegian Sea to the Chukchi Sea and then somewhat declines in the Beaufort Sea. Species of Pacific origin outnumber those of Atlantic origin only in the Chukchi and Beaufort Seas. In the East-Siberian Sea the number of species of different origin is equal.

In all deep-sea regions the share of species of the Atlantic origin is much higher than that of the Pacific origin.

Discussion

Two different approaches were used in the present study to identify the region of penetration of bivalve species into the Arctic Basin. Both of them, the first based on the modern distribution and the second based on paleo-data, gave similar results. Among 104 genera, the results of the two approaches agreed for 86 genera (83%). This high degree of coincidence indicates the reliability of the criteria used.

The results suggest that most of the Recent Arctic bivalves are of Atlantic origin. To test this conclusion, we conducted additional analysis with an enhanced weighting of criteria supporting the Pacific origin. Even in this case, the genera and species of Atlantic origin clearly prevailed.

Our results (Table 2), in principle, agree with data of Fedyakov and Naumov (1987) for the whole Arctic. According to these authors, a minimum of 55% of species are of Atlantic origin and a minimum of 12% are of Pacific origin. However, other authors came to different conclusions. Filatova (1957a) agreed that species of Atlantic origin have the larger share, but she also believed that the impact of autochthonous species was very high. According to Kafanov (1979), species of Pacific origin dominate: 70% compared with 17.5% of North Atlantic origin and with about 12.5% of species of unclear origin. Kafanov (1979) explained the similarity of modern faunas of the Arctic and the North Atlantic by the fact that many Arctic species are secondarily Atlantic by origin. Ancestors of such species migrated from the North

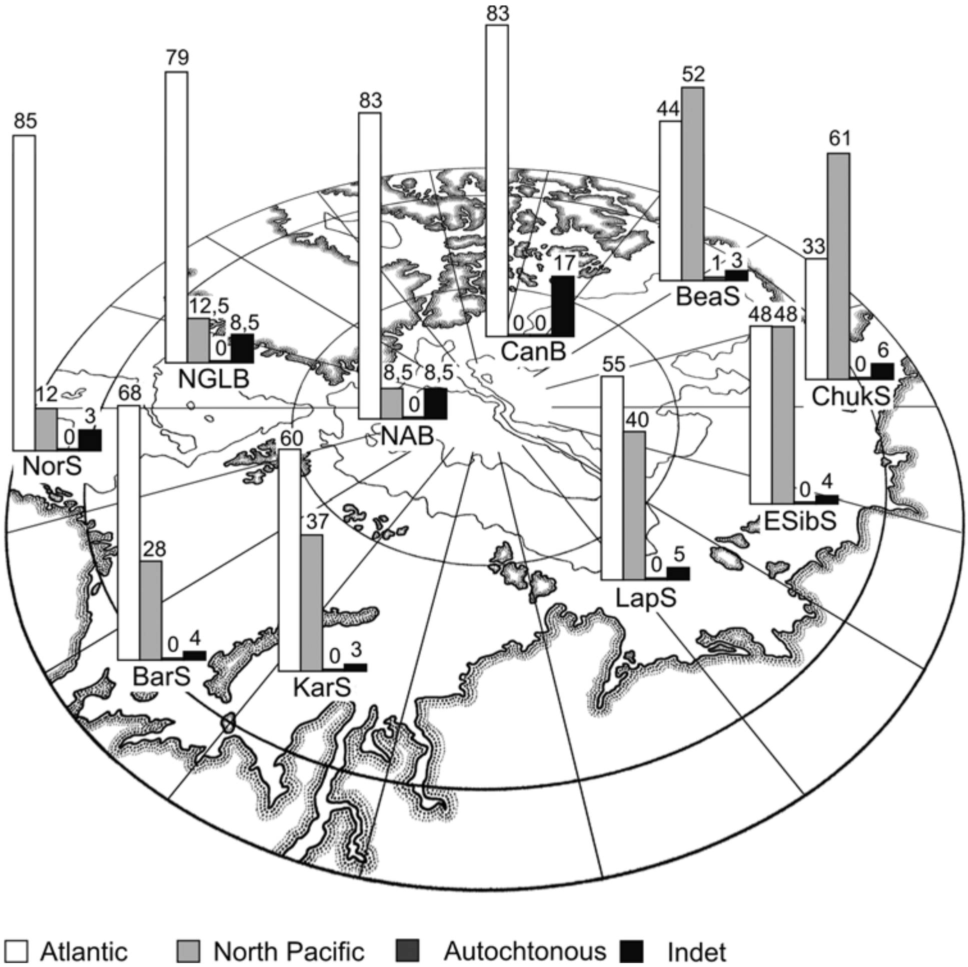


Fig. 4. Percentage of Bivalvia species of different origin in various Arctic regions.
Abbreviations: see Fig. 1.
Рис. 4. Процентное соотношение видов двустворчатых моллюсков различного происхождения в разных регионах Арктики.
Обозначения те же, что на Рис. 1.

Pacific through the Arctic to the North Atlantic and then, during periods of climate warming, these species or their derivatives colonized the Arctic from the North Atlantic.

These discrepancies between the results of different authors may in part be explained by differences in the methods used. For example, Filatova (1957a) did not include the Norwegian Sea in the analysis, thus she excluded a number of species of Atlantic origin. In addition we assigned many of Filatova's autochthonous Arctic species to genera of Atlantic or Pacific origin, depending on the biogeographical history of a genus (see Materials and Methods). According to our approach, only species of endemic Arctic genera were considered as truly autochthonous. Unfortunately, we cannot compare our methods with the approach of Kafanov (1979) since he did not describe it in sufficient detail.

The present results differ from those for shelf starfish. In the Arctic Asteroidea, the prevalence of taxa of Pacific origin was shown by Djakonov (1945) and Mironov, Dilman (2010). Mironov and Dilman (2010) used the same criteria as used in the present study to identify

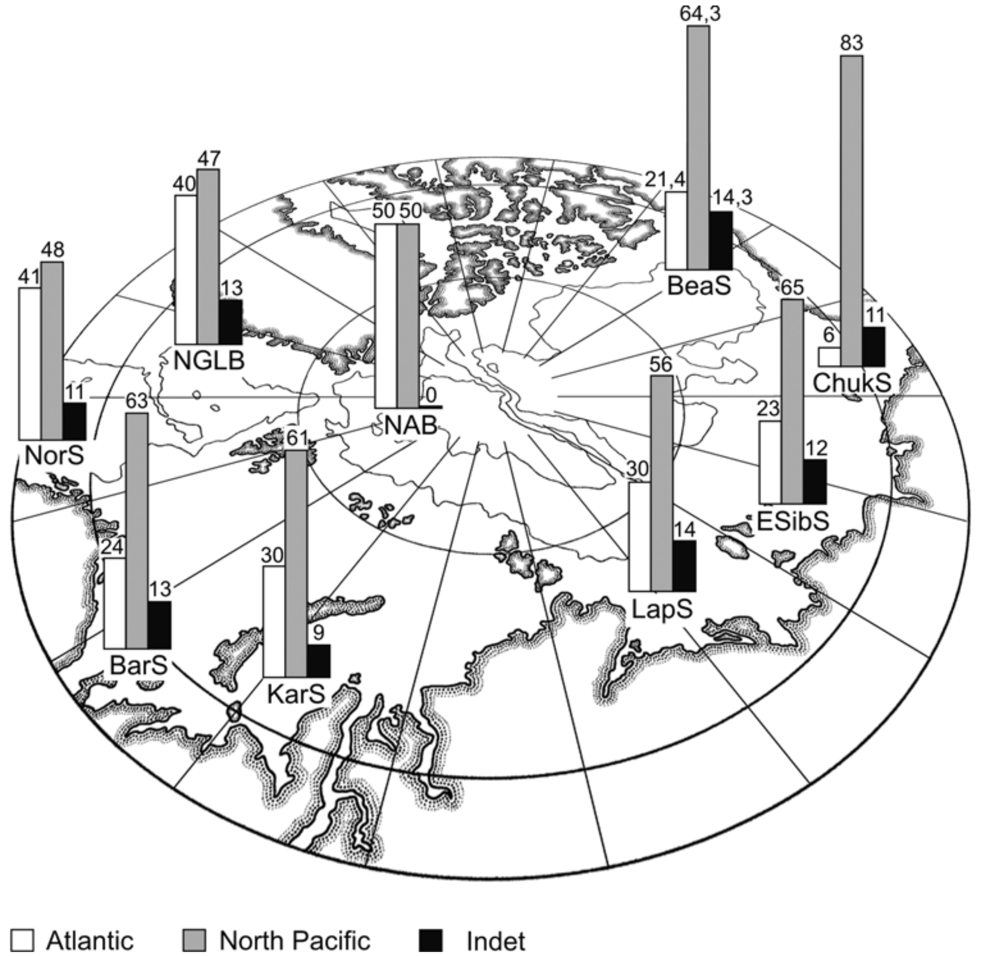


Fig. 5. Percentage of species of Asteroidea of different origin in various Arctic regions (after Mironov, Dilman, 2010).
Abbreviations: see Fig. 1.
Рис. 5. Процентное соотношение видов морских звезд различного происхождения в разных регионах Арктики.
Обозначения те же, что на Рис. 1.

the origin of genera (Fig. 5). Thus, different proportions of genera of the Atlantic and the Pacific origin are most likely taxon-specific and reflect the different biogeographic history of bivalve molluscs and sea stars in the Arctic. Differences in the patterns of modern regional distribution of bivalves and starfish in the Northern Hemisphere support such assumption. For example, the share of genera recorded in the North Atlantic and in the Arctic, but unknown from the North Pacific, is higher in bivalves than in sea stars: 45 and 31% respectively. Genera of sea stars unknown from the North Pacific are characterized by a low number of species in the North Atlantic: usually 1–3 (5 species only in the case of *Poraniomorpha*). Genera of bivalves unknown from the North Pacific often contain more than three species in the North Atlantic, the maximum being 10 species in *Parvicardium*.

The different biogeographic history is apparently associated with a different evolutionary plasticity in the two taxa. The evolutionary plasticity of Bivalvia is higher than of Asteroidea. The higher number of species, in bivalve

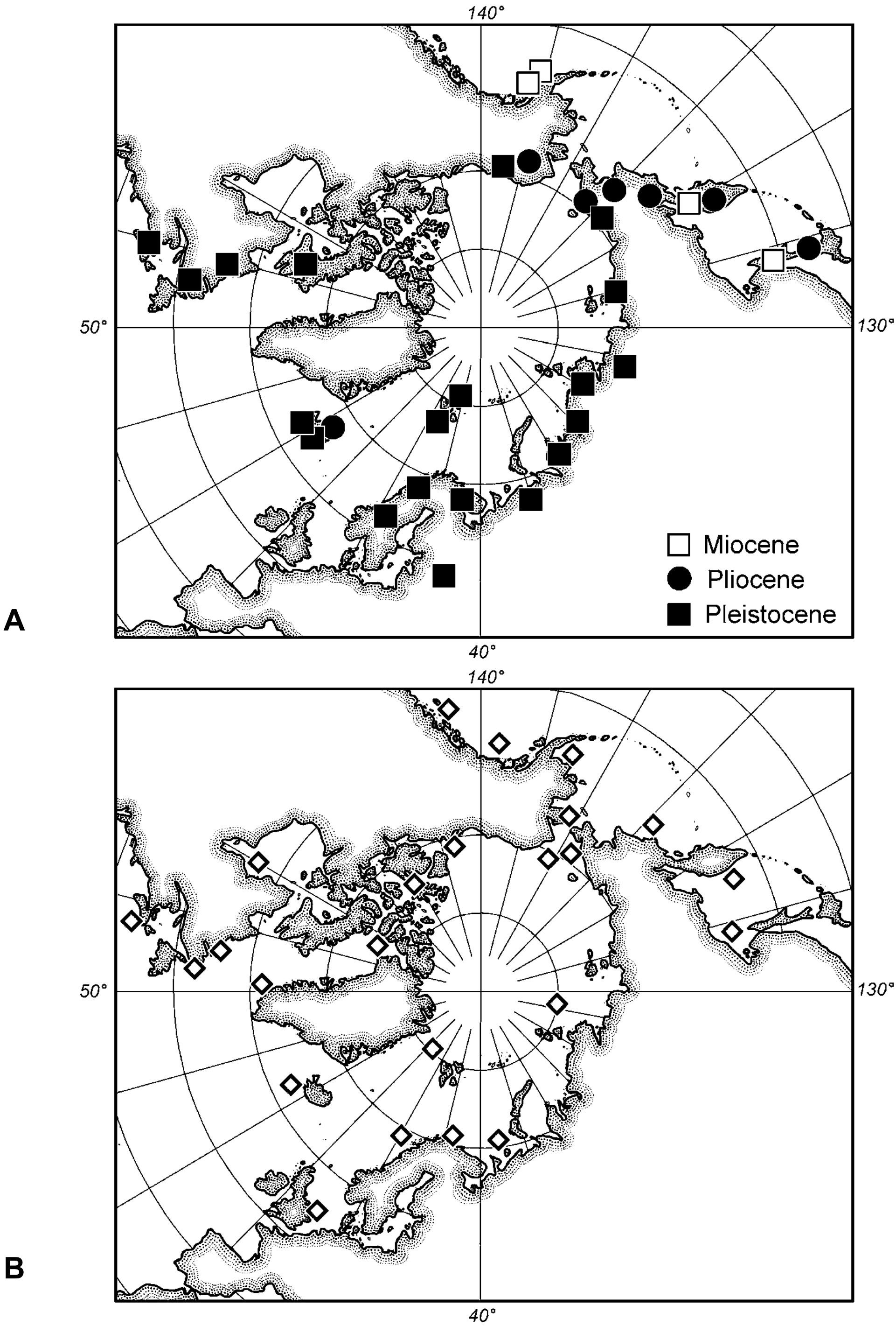
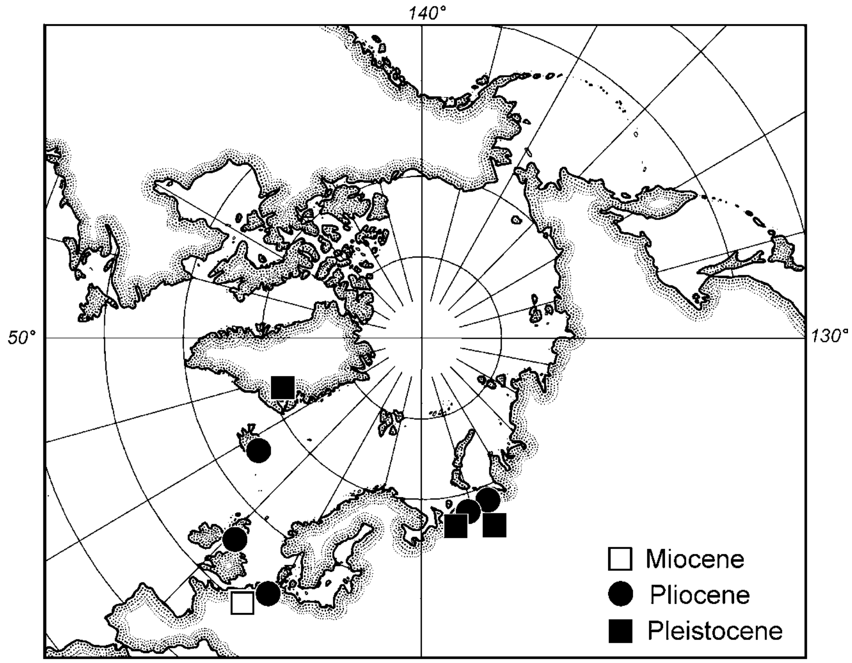
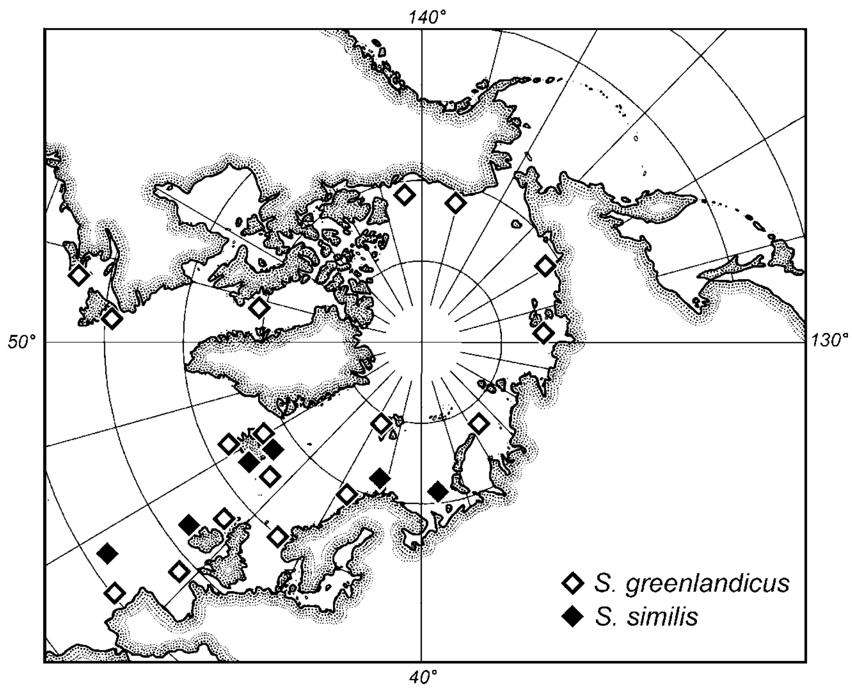


Fig. 6. Paleo-records and recent distribution of the genus *Ciliatocardium* Kafanov, 1974.
A — paleo-records (after Kafanov, 1980; Kafanov et al., 2001); B — recent distribution in the Arctic.
Рис. 6. Палео- и современное распространение двустворчатых моллюсков рода *Ciliatocardium* Kafanov, 1974.
A — палео-нахождения (по Kafanov, 1980; Kafanov et al., 2001); B — современное распространение в Арктике.



A



B

Fig. 7. Paleo-records and recent distribution of the genus *Similipecten* Winckworth, 1932.

A — paleo-records (after Gladenkov, 1978; Merklin et al., 1979; Marquet, 2002); B — recent distribution in the Arctic.

Рис. 7. Палео- и современное распространение двустворчатых моллюсков рода *Similipecten* Winckworth, 1932.

А — палео-нахождения (по Гладенков, 1978; Мерклин и др., 1979; Marquet, 2002); В — современное распространение в Арктике.

molluscs as a whole, shows this. During periods of glaciation, the most pronounced changes in the marine environment occurred in the North Atlantic and in the near-Atlantic Arctic. Evolutionary flexible groups, such as bivalves, would be expected to be more successful in periods of rapidly changing environment and quicker in restoring their diversity.

According to numerous published data, the trans-Arctic exchange between faunas of the North Atlantic and the North Pacific was asymmetrical: the number of colonists from the Pacific was higher than the number of colonists from the Atlantic (Andriyashev, 1939; Durham, MacNeil, 1967; Kafanov, 1979; Vermeij, 1991). Possible reasons for this asymmetry were discussed by Vermeij (1991). Our data on Recent Arctic bivalves confirm this asymmetry of trans-Arctic migration. The number of genera having crossed the Arctic from the Pacific is 1.4 times higher than that from the Atlantic. The fact of prevalence of species of Atlantic origin in the Arctic, along with higher share of genera of Pacific origin in the trans-Arctic migration requires explanation. Most of the genera of the Pacific origin that crossed the Bering Strait (69%) penetrated also the North Atlantic. On the contrary, only 14% of the Arctic genera of the Atlantic origin occur also in the North Pacific. Thus, most taxa that penetrated the Arctic from the North Pacific participated in the trans-Arctic exchange, whereas most taxa of the Atlantic origin remained within the Arctic Ocean.

These differences in dispersal patterns of taxa of the Atlantic and the Pacific origin might be related to features (nature) of barriers for dispersal. It can be suggested that the boundary between the Arctic and the Atlantic can be easier penetrated in both directions than the Bering Strait. The area of contact of the Arctic and the Atlantic faunas is much wider than the Arctic-Pacific zone of contact and also there are various deep-water straits between the North Atlantic and the Arctic. The connection between the Arctic and the Pacific is narrow and shallow-water, thus more effective as a barrier. The Bering Strait as a barrier is asymmetric, colonization from the North Pacific to the Arctic is more intensive than from the Arctic to the North Pacific. The prevailing northward trend of colonization from the North Pacific could have two reasons. According to Briggs (1974), in interaction of two faunas colonization occurs mainly from an area with higher diversity (in our case the North Pacific) towards an area with lower diversity. Second, the Bering Strait was opening in periods of transgression and climate warming which also determined the prevailing northward dispersal.

According to our results the majority of deep-sea species belong to genera of Atlantic origin. This is true for all the three studied deep-sea regions. Among shallow-water regions, only in the Norwegian Sea is the share of species of Atlantic origin higher. A characteristic feature of the Arctic deep-sea basins is the relatively high number of endemic species in genera of Atlantic origin.

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