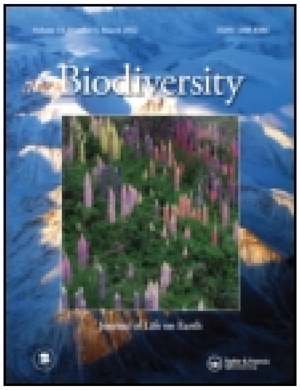

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Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades

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Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades

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The warming of Arctic waters over the last decades has been confirmed by the results of numerous studies. New data on distribution of cephalopods in the Arctic were obtained from the research cruises of PINRO (Russia) and IMR (Norway) during 2006–2011. *Teuthowenia megalops* and *Todaropsis eblanae* were found in the Arctic for the first time, at distances of more than 1000 km and 2500 km outside of their ranges, respectively. The demersal species *T. eblanae* inhabiting the lower shelf and upper continental slope has presumably spread into the Barents Sea by the eastern branch of the Norwegian Current, and further by the southern branch of the North Cape coastal current, as far as the Murman shelf. The bathypelagic species *T. megalops* is carried to the Arctic evidently by the deep-water warm Atlantic Currents. The new spreading areas of both species are obviously the non-reproductive zones of their ranges. Foraging shoals of *Todarodes sagitatus* were recorded in the Arctic in 2010 for the first time in the last 25 years, which can be related to not only the warming of Arctic waters, but also the fluctuation of *Todarodes* levels in the main part of the range in the Northern Atlantic. The native Arctic species *Gonatus fabricii* has expanded its range to the eastern part of the Barents Sea and to the adjacent part of the Kara Sea. In these areas of Arctic waters, warming is particularly noticeable and the ongoing climatic changes are leading to boreal cephalopods spreading into the Polar Basin. This may impact species relations in vulnerable Arctic ecosystems.

Keywords: Cephalopoda; warming of Arctic waters; *Todaropsis eblanae*; *Teuthowenia megalops*; *Todarodes sagittatus*; *Gonatus fabricii*

Introduction

Research into the study and preservation of the unique and highly vulnerable ecosystems of the Arctic regions has recently become a priority due to the growing interest of many countries in the resources of the polar shelf. Thus, changes in hydrological conditions in Arctic regions have become the focus of studies in recent decades. Warming of the Arctic waters is thought to be closely connected with heat content increase of the Atlantic water masses (Walther et al. 2002; Hassol 2005; Polyakov et al. 2005; Boitzov 2006, 2009; Walczowski and Piechura 2006; Walsh 2008). The waters are transported to the Arctic Basin by the Norwegian current, and then divided between the warm North Cape (one-third of the Norwegian current's volume) and West Spitsbergen currents around the Mohns Ridge. The former enters the Barents Sea, where almost 88% of the transported heat is spent (Dobrovolsky and Zalogin 1982). The West Spitsbergen current plays a major role in warming the waters of the Arctic region as a whole. The mid-annual water temperature of the Atlantic layer (depth 200–800 m) in the current's northern part has increased by 1.32°C from 1990 to 2005 (Walczowski and Piechura 2006). As a consequence, all the Arctic waters are now affected by warming to different degrees (average mean rise of 0.8°C). The mid-annual temperature of the surface water layer (0–200 m) in the Barents Sea has increased by 0.5°C since 1990 (Boitzov 2006, 2009). Additionally, in recent years a tendency towards disappearance or easing of the cold halocline phenomenon in the Eurasian Basin has been observed (AARI 2011).

Cephalopods are one of the essential components of Arctic sea ecosystems. However, the environmental conditions in the Arctic are not the most favourable for their persistence (Nesis 2001; Gardiner and Dick 2010). Species composition, taxonomy, distribution and biology of Arctic teuthofauna are not well studied. About ten species of cephalopods are known to live permanently in the Arctic: sepiolids *Rossia palpebrosa* Owen, 1834 and *R. moelleri* Steenstrup, 1856; squid

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Gonatus fabricii (Lichtenstein 1818); cirrate octopus *Cirroteuthis muelleri* Eschricht, 1838; incirrate octopuses *Bathypolypus arcticus* (Prosch 1849), *B. bairdii* (Verrill 1873), *B. pugniger* Muus, 2002, *Benthoctopus johnsonianus* Allock, Strugnell, Rigeiro and Collins, 2006, *B. normani* (Massy 1907) and *B. sibiricus* Loyning, 1930 (Nesis 1987; Muus 2002; Allock et al. 2006). The problem with taxonomy and validitating the status of *Bathypolypus* and *Benthoctopus* species at present remains unsolved and is not discussed further in this article. In addition to these ten native species, 28 other cephalopod species are documented as spreading or already spread into the Arctic and subarctic waters (Table 1). We suggest that 11 of these species are wrongly identified and that only three species among decapod cephalopods have spread into Arctic waters: *R. megaptera*, *Illex illecebrosus* and *T. sagittatus*. Further additions for this species list are as follows: lesser flying squid *T. eblanae* (Ball 1841), recorded in the Arctic for the first time in 2006 (Sabirov, Lubin, and Golikov 2009), and *T. megalops* (Prosch 1849), recorded in the northernmost point in the Arctic in 2009 (Golikov et al. 2012). Also, *T sagittatus* was found on the border of the Norwegian and Barents Seas in 2011 for the first time since 1983 (Nesis 1987; Jørgensen, Anisimova, and Storeng 2012). The most abundant Arctic pelagic cephalopod, *G. fabricii*, has a well-established increase in its range as well.

Increased temperature and salinity create favourable conditions for distribution of cephalopods, which as a whole are a thermophilic group of sea invertebrates, preferring water with oceanic salinity levels. The occurrence of boreal cephalopod species in the Arctic and the increase in native cephalopod species ranges are clearly connected with the climatic changes of recent years. The primary objectives of this paper are to describe changes in Arctic teuthofauna distribution during the last decade by the use of field data, combined with a literature research.

Materials and methods

The material was collected by research vessels of PINRO (RV ‘Smolensk’, ‘Vilnius’, ‘F. Nansen’) and IMR (RV ‘Jan-Mayen’) in 2006–2011 from the Barents Sea, the western part of the Kara Sea, the northeastern parts of the Norwegian and the Greenland Seas, and an adjacent part of the Central Polar Basin (68°30′–82°00′ N; 4°30′–72°00′ E). Specimens were caught by bottom trawl ‘Campelen-1800’ at depths to 1450 m and by pelagic trawl ‘Harstad’ at depths to 100 m. Twenty-one specimens of *T. eblanae*, two specimens of *T. megalops*, three specimens of *T. sagittatus* and 734 specimens of *G. fabricii* were collected. Samples were fixed in 4% formaldehyde. Dorsal mantle length (ML), body weight, sex and stage of maturity were estimated onboard. Cameral treatment took place in the Laboratory of Hydrobiology of Kazan University, and included detailed analysis of the reproductive system: measurement and weight of the reproductive system and its individual components, fecundity investigation, and calculation of the main reproductive indexes.

Statistics were calculated using the programs Statgraphics 5.0 and MS Excel. Mann–Whitney test (U) was determined together with other statistical indexes.

Results

Lesser flying squid Todaropsis eblanae

T. eblanae was caught in the Barents Sea on the Murman shelf (71°13′ N, 36°38′ E) (Figure 1a) for the first time in August 2006 (Sabirov, Lubin, and Golikov 2009). A single specimen was caught during horizontal trawling at 0–60 m at the location with depth of 225 m at 2 a.m. This species was previously recorded near the southern coast of Norway at 61°15′ N (Zumholz and Piatkowski 2005) more than 2000 km further southwest. In August 2008, the lesser flying squid was photographed on the Murman shelf (69°40′ N, 34°26′ E) by SCUBA divers from PINRO (the head was S. Rusyaev). *T. eblanae* were recorded at about 15 m depth in the sublittoral zone, which is unusual for this species in the main part of its range (Adam 1952; Roper, Nigmatullin, and Jereb 2010). In September 2010, 19 specimens of lesser flying squid were caught on the northern continental slope of the Norwegian Sea near the border to the Barents Sea (73°34′ N, 15°33′ E). These findings suggest that the appearance of *T. eblanae* in the Arctic has been a continuous process in recent years. Lesser flying squid probably does not reach sexual maturity in the new part of its range, and has an abnormal development of its reproductive system in unusual conditions (Sabirov, Lubin, and Golikov 2009).

European flying squid Todarodes sagittatus

Foraging shoals of *T. sagittatus* have been recorded in the Arctic since 1874 (Derjugin 1915; Kondakov 1937). The northern border of the main part of its range is the Faroe-Shetland threshold and the southern part of the Norwegian Sea (~62°N) (Clarke 1966; Nesis 1987). Sometimes foraging shoals, mainly of immature females, spread into Arctic waters. These pulses of spreading usually persist for one to five years, with a periodicity of less than 10 years. On the Norwegian

Table 1. List of subtropical and boreal species of cephalopods recorded in Arctic and subarctic waters.

No.	Species	The northern border of known range	Places of new finding	References
Order Sepiolida				
1	*Rossia macrosoma* (delle Chiaje, 1829)	Faroes, shelf of Norway to ~60°N	Iceland, shelf of Norway to ~66°N	Grimpe 1933; Reid and Jereb 2005
2	*R. megaptera* Verrill, 1881	Davis strait	Western and Eastern (?) Greenland	Mercer 1969; Nesis 1987
3	*R. pacifica* Berry, 1911	Bering slope	Bering shelf	Akimushkin 1965; Reid and Jereb 2005
4	*Semirossia tenera* (Verrill, 1880)	Nova Scotland	Kara Sea; Spitsbergen	Grimpe 1933; Kondakov 1948
5	*Sepietta scandica* (Steenstrup, 1887)	Southern Iceland, shelf of Norway to ~60°N	Iceland, shelf of Norway to ~70°N	Grimpe 1933; Reid and Jereb 2005
6	*Sepiola atlantica* D'Orbigny, 1839		Iceland	Reid and Jereb, 2005
7	*Sepiola pfefferi* Grimpe, 1921	Faroe-Shetland ridge, shelf of Norway to ~60°N	Shelf of Norway to ~66°N	Grimpe 1925, 1933
8	*S. rondeletii* Leach, 1834		Ellsmere island	Gardiner and Dick 2010
Order Spirulida				
9	*Spirula spirula* (Linnaeus, 1758)	Western Atlantic to ~45°N	Canadian shore, 69°44′N	Mercer 1969
Order Teuthida				
10	*Architeuthis dux* Steenstrup, 1857	Newfoundland; Faroe-Shetland ridge	Western Greenland (~67°N), shelf of Norway to ~70°N	Pfeffer 1912; Muus 1959; Nesis 1987
11	*Berryteuthis magister* (Berry, 1913)	Bering slope	Bering shelf, Anadyr gulf	Akimushkin 1965
12	*Brachioteuthis riisei* (Steenstrup, 1882)	Faroe-Shetland ridge, northern part of the North Sea	Norwegian Sea (to 68°34′N, 6°01′E)	Pfeffer 1912; Grimpe 1933; Mercer 1969; Nesis 1987
13	*Gonatus steenstrupi* Kristensen, 1981	Denmark strait, Faroe-Shetland ridge	To the north from Denmark strait	Kristensen 1981
14	*Illex illecebrosus* (Le Sueur, 1821)	Southern Labrador; to Davis and Denmark straits (foraging shoals)	Baffin Sea; north Iceland	Pfeffer 1912; Grimpe 1933; Mercer 1969; Nesis 1987
15	*Ommastrephes bartrami* (Le Sueur, 1821)	Southern slope of Grand Banks of Newfoundland; Faroe-Shetland ridge, northern part of the North Sea	Spitsbergen; Davis strait	Grimpe 1933; Kondakov 1948
16	*Onychoteuthis banksi* (Leach, 1817)	Northern part of the North Sea	Shelf of Norway to ~70°N	Sars 1878
17	*Onykia robusta* (Verrill, 1876)	Bering slope	Bering shelf, Chukchi Sea	Kondakov 1948; Mercer 1969
18	*Teuthowenia megalops* (Prosch, 1849)	Davis and Denmark straits, Faroe-Shetland ridge	Baffin Sea (~73°N); 65–66°N in Denmark straits and 62–63°N in the Norway Sea	Pfeffer 1912; Nesis 1965; Voss 1985
19	*Todarodes sagittatus* (Lamarck, 1799)	Faroe-Shetland ridge, southern part of the Norway Sea (~62°N)	Norway and Barents Sea; rarely to the White and Kara Seas (foraging shoals)	Grimpe 1933; Kondakov 1937; Muus 1959; Wiborg et al. 1982
Order Octopoda				
20	*Cirrothauma* sp.	Subtropical Atlantic	Central Polar basin (86°N, 173°E)	Nesis 1987

(*continued*)

Table 1. Continued.

No.	Species	The northern border of known range	Places of new finding	References
21	*Opisthoteuthis borealis* (Collins, 2005)	Range is not known completely, North Atlantic	Western and Eastern Greenland	Collins 2002, 2005
22	*Benthoctopus hokkaidensis* (Berry, 1921)	Bering slope	Bering shelf, Chukchi Sea	Kondakov 1948; Akimushkin 1965; Nesis 1987
23	*B. profundorum* Robson, 1932	Bering slope	Bering shelf, Chukchi Sea	Kondakov 1948; Akimushkin 1965; Nesis 1987
24	*Benthoctopus* sp.	Bering slope	Bering shelf, Chukchi Sea	Kondakov 1948; Akimushkin 1965; Laptikhovsky 1999
25	*Eledone cirrhosa* (Lamarck, 1798)	Faroes, Southern Iceland	Northern Iceland, Shelf of Norway to ~ 70°N	Grimpe 1933; Muus 1959
26	*Graneledone verrucosa* (Verrill, 1881)	Ocean Ridge slope near Southern Iceland	Denmark strait	Grimpe 1933; Muus 1959
27	*Octopus leioderma* (Berry, 1912)	Bering slope	Bering shelf, Chukchi Sea	Kondakov 1948; Akimushkin 1965; Nesis 1987
28	*Sasakiopus salebrosus* (Sasaki, 1920)	Bering slope	Bering shelf, Chukchi Sea	Conners, Conrath, and Aydin 2011

Note: Grey stripe – mistakenly recorded species.

shelf, *T. sagittatus* appear more often. Foraging shoals of European flying squid were recorded from the White Sea twice in 1884 and 1980, and once from the Kara Sea in 1932, as far as Severnaya Zemlya Archipelago (Kondakov 1937; Akimushkin 1965; Wiborg, Gjøsaeter, and Beck 1982). *T. sagittatus* has not been recorded in Arctic waters since 1983 (Sundet 1985; Nesis 1987). However, in September 2010, during horizontal trawling from 300 m to the surface, *T. sagittatus* was caught again in the northeastern part of the Norwegian Sea (73°34′ N, 15°33′ E) and in the southwestern part of the Barents Sea (73°57′ N, 21°26′ E) (Figure 1b). Sampled specimens show the ML less than 10 cm, although foraging shoals in earlier years consisted of larger squids with an average ML of 22–26 cm (Wiborg 1984).

Atlantic cranch squid Teuthowenia megalops

Two specimens of *T. megalops* were caught in May 2009 in the bathypelagic zone (trawling depth 1400 m) on the northeastern slope of the Norwegian Sea (73°48′ N, 14°31′ E) (Figure 1c). This is the most northerly point at which this species has been caught to date. This point is removed by almost 1000 km from the known border of the range in the Eastern Atlantic (Voss 1985; Roper and Jereb 2010). Sampled specimens were maturing females with undeformed arms, ML 24–26 cm. Nesis (1965, 1987) has referred to the possible existence of non-reproductive spreading zones of *T. megalops* in the Eastern Atlantic to the north of the Denmark Strait, and in the Western Atlantic to the north of the Davis Strait as far as the central basin of the Baffin Bay.

Boreoatlantic gonate squid Gonatus fabricii

G. fabricii is the most abundant squid in the high latitudes of the Atlantic, with an enormous arctic-boreal range. It is the only native pelagic species of cephalopods in the Arctic. This squid inhabits the central part of the Polar Basin, the shelf of the western and central parts of the Barents Sea, the Norwegian and Greenland Seas, Baffin Bay, and the Davis and Denmark Straits. Southward it reaches Cape Cod in the Western Atlantic and the North Sea in the Eastern Atlantic. Occurrence on the eastern part of the Barents Sea shelf and on the shelves of the East Arctic seas has never before been reported (Kristensen 1984; Nesis 1987, 2003; Gardiner and Dick 2010) (Figure 1d).

The new parts of the *G. fabricii* range reach the edge of the Novaya Zemlya shallow area in the eastern part of the Barents Sea, and the Svyataya Anna Trough in the western part of the Kara Sea. Epipelagic juveniles were absent in these areas, and all squids were caught deeper than 250 m in the mesopelagic layer. In the mentioned new parts of the range in the Barents Sea, larger squids (mean size ML 8.3 cm; $U = 33$;

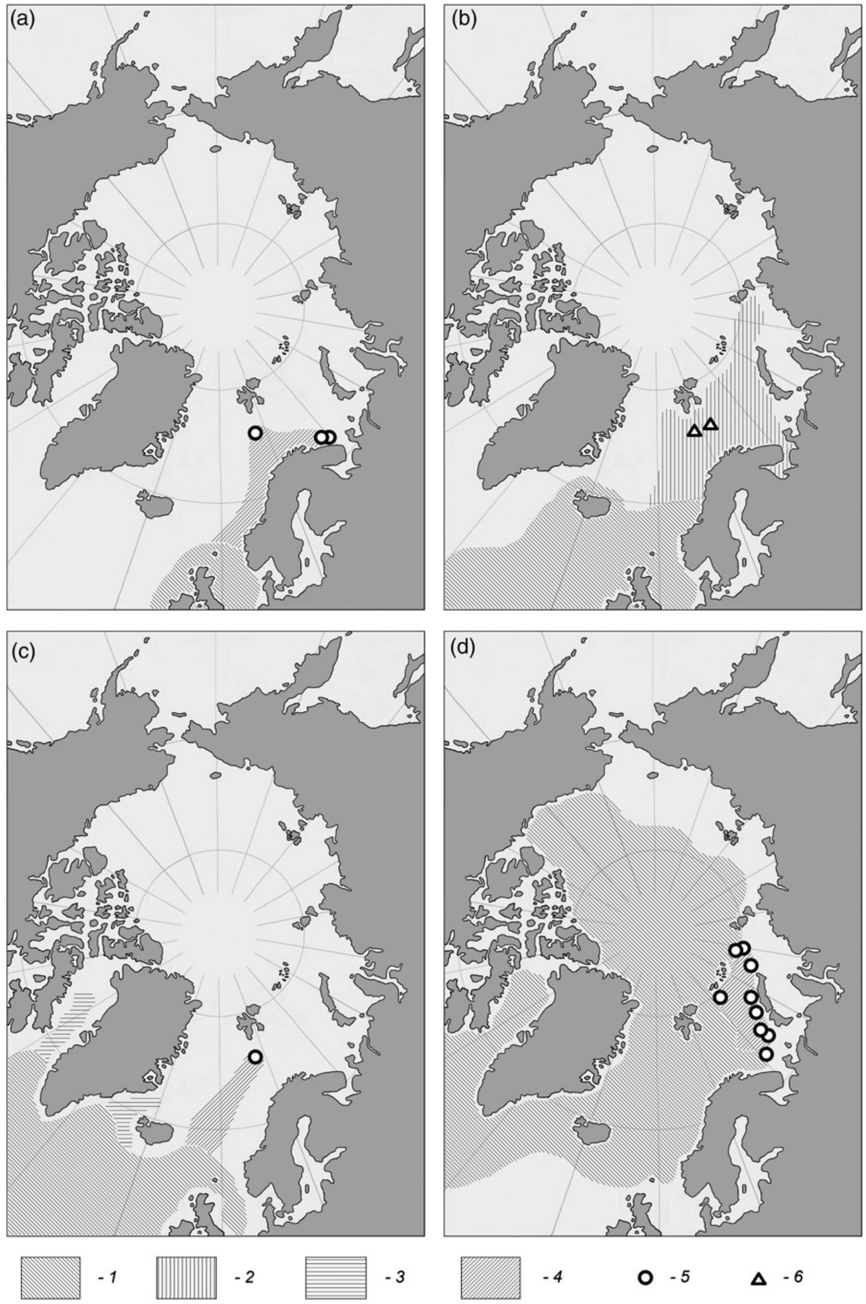

Figure 1. Distribution in the North Atlantic and the Arctic indicating places of capture outside of the main range: *Todaropsis eblanae* (a), *Todarodes sagittatus* (b), *Teuthowenia megalops* (c), *Gonatus fabricii* (d). Key: *1* – known ranges before 2006 according to the literature; *2* – the furthest border of rare spreading of *T. sagittatus* foraging shoals into Arctic; *3* – non-reproductive zone of *T. megalops* bearing out from the main part of its range; *4* – new parts of squid ranges in Arctic; *5* – new points of squid catches outside of known ranges; *6* – *T. sagittatus* catches in 2010.

$p < 0.01$) significantly prevailed if compared with other investigated areas in the Barents and Greenland Seas (ML 4.7 cm). Even larger specimens were observed (ML 9.1 cm; $U = 27$; $p < 0.01$) in the Svyataya Anna Trough. This continuous gradual increase of the squid sizes indicates their probable age migration in the direction of the central Polar Basin.

Discussion

All boreal species of cephalopods were found in the Arctic in the zone of the greatest influence of the Atlantic water masses. *T. megalops* and *T. eblanae* are not active nektonic swimmers, nevertheless, both species were found in the Arctic, at distances of more than 1000 km and 2500 thousand km, respectively, outside of their known ranges; specimens of these species can be carried by currents for a long time. The time of year from May to August is the period of maximal activity of the Atlantic currents inflowing to the Arctic (Aagaard 1989).

The lesser flying squid *T. eblanae* is a shelf-upper slope demersal species, and has spread into the Barents Sea presumably by the eastern branch of the Norwegian current, and further by the southern branch of the North Cape current as far as the Murman shelf. *T. eblanae* also spread over the continental slope of the Norwegian Sea and further to the west of Medvezhyi Island, evidently via the Western-Spitsbergen current. It was established, that water temperature influences the quantity of *T. eblanae*, while in warmer years its abundance is higher on the shelf of the European seas (Gonzales, Rasero, and Guerra 1994; Hastie et al. 1994; Robin et al. 2002). *T. eblanae* is suspected to have spread in the Arctic several years before 2006, when the first specimens were caught, due to the earlier warming of the Arctic waters. However, because of the typical low abundance of lesser flying squid (Lordan 2001; Roper, Nigmatullin, and Jereb 2010), they were rarely caught by trawling and were probably misidentified when caught. The documented squids from the Arctic are suspected to belong to the nearest North Atlantic population group (Hastie et al. 1994) and the new part of the range a zone of non-reproductive spreading.

T. megalops is carried into the Arctic possibly by the deep warm Atlantic Waters, which move slowly towards the Arctic through the deep parts of the Norwegian Sea (Blindheim 1990). This species inhabits the bathypelagic zones where the warmest waters of the Atlantic penetrate into Arctic waters. Atlantic cranch squid is a boreal-subtropical thermophilic species (Voss 1985; Roper and Jereb 2010). During recent decades the zone of non-reproductive dispersal of this species has extended from the Denmark Strait into the Arctic as far as the slope of the north-eastern Norwegian Sea.

For *T. sagittatus* the relationship between the distribution and the temperature is not so evident. Its penetration into the Arctic has occurred both in warm-water and in cold-water years. The hydrological preferences are still largely unknown (Wiborg, Gjøsaeter, and Beck 1982; Boitzov 1984; Wiborg 1984; Sundet 1985). Abundance of the European flying squid on the European shelf increases in colder years, exactly when the quantity of *T. eblanae* decreases (Hastie et al. 1994). So, the above-mentioned finding of *T. sagittatus* in 2010 can be connected not only with warming of the Arctic waters, but also with some other factors which influence the reproduction of this species in the main part of its Northern Atlantic range.

The increase in the range of the native arctic species *G. fabricii* into the eastern part of the Barents Sea and to the adjacent area of the Kara Sea has been documented. In these parts of the Arctic waters, warming is particularly noticeable. Warm Atlantic water penetrates into the Arctic at the meso- and bathypelagic layers. This depth (200–800 m) is also inhabited by maturing specimens of *G. fabricii* and through these warm water masses, this species has spread into the eastern part of the Barents Sea and into the Svyataya Anna Trough in the Kara Sea. The salinity is too low ($<25‰$) for *G. fabricii* to spread into the southeastern part of the Barents Sea (so-called 'Pechora Sea') due to the large river drain into this area. From the western part of the Barents Sea to its eastern section and to the Svyataya Anna Trough there is a gradual increase in the size of immature and maturing specimens. This represents an age migration towards the central Polar Basin, where the reproduction zone of *G. fabricii* is found (Young 1973; Nesis 1987). The increase of its range on the shelf leads to the foraging zone widening and approaching the reproductive zone. Thus, the relationship between the expanding species range and the warming water masses is clear.

Global climatic change is responsible for increased temperatures in Arctic waters. As a whole, this is favourable for the Arctic dispersal of new species of cephalopods and for an increase in their abundance and changes in the functional structure of their ranges. However, considering the high vulnerability of Arctic ecosystems, these changes will impact the balance between species in ecosystems across the entire Polar Basin.

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