

Distribution and growth of bivalve molluscs *Macoma calcarea* (Gmelin, 1791) in the Kara Sea

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Abstract

This study is devoted to the analysis of distribution and linear growth of *Macoma calcaria* in the southwestern part of the Kara Sea based on the results of observations (119 stations at depths from 4 to 415 m) in August-September 2012–2013. It appeared that for at least the last 100 years *M. calcaria* has been a characteristic component of coastal bottom communities in the southwestern part of the Kara Sea and sometimes dominated by biomass. The densest beds of *M. calcaria* were confined to the silty biotopes at depths less than 50 m. Within this depth range, it was possible to associate the distribution of molluscs only with the characteristics of bottom sediments. The highest values of *Macoma* biomass and density (up to 90 g m^{-2} and 120 ind. m^{-2} , respectively) differed in habitats with a rather high content of silt in the bottom sediments (more than 80%), which quite logically corresponded to the trophic characteristics of this species. The influence of interspecific relationships on the distribution of *Macoma* was not revealed. The maximum size and age of *M. calcaria* (37 mm and 21 years, respectively) in the southwestern part of the Kara Sea, the average annual growth rate (about 2 mm/year) turned out to be close to those of this species in other areas of distribution. It was shown that the results of the age determination of specimens by the external morphology and inner marks (shell cross-sections) were quite comparable. Individual and group growth of *Macoma* were characterized by weak heterogeneity within the studied water area. The individual growth of molluscs, apparently, is mostly determined by the characteristics of the initial period of molluscan growth.

1. Introduction

In recent decades, the explorations of the marine biota in the Arctic Seas have accelerated substantially, which is associated with intensification of oil and gas field development in the Arctic shelf zone. An industrial development is impossible without environmental monitoring, which should start from the selection of observation objects. The most attractive monitoring objects in the Arctic seas are the populations of widespread bivalve molluscs. These animals have a number of features, which made them the convenient model objects for ecological monitoring. They are characterized by the ability to form sufficiently dense aggregations accessible for exploration, the relatively long lifespan of some species, and the specific shell morphology, which allows their age determination. The bivalves are often edificatory species. However, the population properties of many common Bivalvia in the Arctic seas are relatively poorly studied.

The widespread boreal-arctic circumpolar bivalve *Macoma calcaria* (Gmelin, 1791) is a typical example of such species. It is one of the most common bivalves in the infauna of all Arctic seas of Russia. *M. calcaria* often dominates by biomass in some soft-bottom communities (Filatova & Zenkevich 1957; Antipova & Semenov 1989; Kiyko & Pogrebov 1997; Kamenev et al. 2004; Sirenko & Gagaev 2007; Britaev et al. 2010). It is capable to form dense (over 100 ind. m^{-2}) beds, which are relatively accessible for study (Babkov & Golikov 1984; Scarlato 1987; Naumov 2006; Sirenko & Gagaev 2007; Gerasimova et al. 2017; Maximovich et al. 2018; Gerasimova et al. 2019; Noskovich 2021). *M. calcaria* beds with a density and biomass of more than 6000 ind. m^{-2} and about 4 kg m^{-2} , respectively, are known from the Chukchi Sea

(Sirenko & Gagaev 2007). These molluscs have a relatively long life span - up to 15–26 years (Petersen 1978; Antipova 1979; Selin 2010; Gerasimova et al. 2019; Noskovich 2021). Thus, the population characteristics of the mollusc can be very indicative in environmental monitoring. As it was noted in the atlas "Species - biological indicators of the state of Arctic marine ecosystems" (Mokievsky 2020), that *M. calcarea* abundance can be useful indicator of the state of the environment. So, it is important to obtain reliable data on the distribution patterns of these molluscs. However the properties of *M. calcarea* populations in the Arctic region have so far been studied very fragmentally. Long-term (more than 20 years) observations of *Macoma* bed structure were undertaken only at the White Sea (Gerasimova & Maximovich 2013; Lisitsyna et al. 2017). For other Arctic regions, the best-known research concerns a short-term (within 3 years) study of *M. calcarea* life cycle in the coastal waters of Western Greenland (Petersen 1978). Detailed studies of the *M. calcarea* distribution have been undertaken only at the White, Barents, and Pechora Seas (Fedyakov 1986; Gerasimova et al. 2019; Noskovich 2021). There is scarce information on the *M. calcarea* growth in Arctic seas (Petersen 1978; Gerasimova et al. 2019; Noskovich 2021). Meanwhile, the growth characteristics of bivalve molluscs reflect the changes in the conditions of local biotopes (both abiotic and biotic), and trends in key environmental variables. Often, even within the same area, the habitat diversity can be reliably assessed via the variation in Bivalvia growth rate, which is sometimes comparable with the variation of growth in the whole species range. However, it should be pointed out that previously published data on the *M. calcarea* growth in the White and Pechora Seas showed a very weak variability in the growth characteristics of these molluscs within some areas, despite obvious differences in environmental conditions (Lisitsyna et al. 2017; Gerasimova et al. 2019).

In 2012–2013 the most detailed (for the entire period of observations) hydrobiological studies have been undertaken in the southwestern part of the Kara Sea (Gerasimova et al. 2021). The study area was covered by a dense grid of stations (almost 120 stations) at depths from 4 to 400 m. *Macoma calcarea* was a common zoobenthos component at depths less than 100 m and sometimes dominated in terms of biomass. In this way, we had a chance to study ecological characteristics of this species. The aim of the present study is to analyze the distribution patterns and growth heterogeneity of *M. calcarea* in the southwestern part of the Kara Sea.

2. Materials And Methods

2.1. Study area and sampling

The Kara Sea, an open marginal part of the Arctic Ocean, is one of the coldest Russian seas. Most of the Sea is located within the shelf. The average depth of the Sea is 111 m, while the maximum depth of 620 m is registered in the northern part of St Anna Trench (Dobrovolsky & Zalogin 1982; Zalogin & Kosarev 1999; Kulakov et al. 2004). Bottom sediments in shallow waters and at underwater elevations are predominantly represented by sands and sandy silt, while troughs and depressions are covered with gray and brown clay silts (Zenkevich 1963). The hydrological regime of the Kara Sea is formed under influence of Atlantic, river, surface Arctic and Barents Sea waters (Zenkevich 1963; Dobrovolsky & Zalogin 1982; Zalogin & Kosarev 1999; Kulakov et al. 2004). The southern and central parts of the Sea are influenced by

the runoff of Ob and Yenisei rivers (Morozova et al. 2013). The Kara Sea receives more than one third of the fresh water discharge into the Polar Basin (Hanzlick & Aagaard 1980; Pavlov & Pfirman 1995). In the northern part of the Sea the hydrological conditions are mainly determined by the influx of surface Arctic waters. The Barents Sea waters penetrate the Kara Sea by bending the Novaya Zemlya archipelago, as well as through the Kara Gates, Yugorsky Shar straits, and thereby affect the hydrological structure of the southwestern part. Relatively warm waters of Atlantic origin enter the Kara Sea along the St. Anna Trench in the west and the Voronin Trench in the east (Zenkevich 1963; Dobrovolsky & Zalogin 1982; Zalogin & Kosarev 1999; Kulakov et al. 2004).

In the Kara Sea, the salinity values and their distribution are mainly determined by the free exchange with the ocean, large river runoff as well as ice formation and melting (Dobrovolsky & Zalogin 1982; Zalogin & Kosarev 1999; Kulakov et al. 2004). The average annual salinity of surface waters ranges from 3–5 in the southern part of the Sea to 33–34 in the northern one. In winter (due to decreased river runoff, ice formation), the salinity of surface waters increases. In the southwest, except for regions directly adjacent to the river mouths, surface salinity approaches 25 to 30, and at the bottom reaches about 34 (Kulakov et al. 2004). In summer the lowest salinities (5–10) are observed in the vicinity of the Ob' and Yenisei estuaries, while in the western Sea part it exceeds 32 (Kulakov et al. 2004).

The ice regime of the Kara Sea is very severe. Ice formation begins in September (in the north) and in October (in the south) (Kulakov et al. 2004). From October to May almost the entire Sea is covered with ice (Gerasimov 1970; Pavlov & Pfirman 1995). The northernmost part of the Sea is covered with ice all year round. The ice-covered Kara Sea very poorly warms up. In winter, under the ice, the surface temperature approaches the freezing point (-1.5 -1.7°C). Subzero temperatures in winter are typical for the entire water column, with the exception of the St. Anna and Voronin Trenches, where relatively warm Atlantic waters penetrate (Hanzlick & Aagaard 1980; Pavlov & Pfirman 1995). In August, ice-free surface waters warm up to +3 +6°C on average, in the warmest southwestern part the surface temperature can rise to +10 +12°C (Mokievsky 2016). The thickness of the heated layer (with positive temperatures) in the western regions of the Sea can reach 60–70 m, while in the eastern regions - only 10–15 m (Mokievsky 2016).

Benthos sampling was carried out from the R/V "Dalnie Zelentsy" at 119 stations in the SW part of the Kara Sea in August and September of 2012–2013 (Online Resource 1–2) (Gerasimova et al. 2021). The coordinates of the stations were determined using GPS navigator. Samples were taken with a van Veen grab (sampling area 0.1 m², three replicates per station), sampling depth varied from 4 to 415 m. Samples were gently sieved through a sieve with 0.7 mm mesh. All animals were sorted from the sediment, preserved in 75% alcohol and subsequently identified to the lowest taxonomic level possible. All specimens of each taxon were counted and weighed (up to 0.001 g; wet weight; molluscs and echinoderms were weighed without decalcification). For further analysis, the abundance and biomass of individual taxa at the stations were averaged by three replicates. The specimens of *Macoma calcaria* were selected from the samples and then used for further analysis.

The abiotic parameters including sediment grain size, near-bottom temperature, salinity, oxygen concentration and pH were determined at each station (Online Resource 2). The grain size analysis was performed using the standard dry-sieve shaking methods (Petelin 1967; Eleftheriou 2013). Oceanographic studies were carried out using SBE 19plus SEACAT PROFILER (temperature and salinity) and BIO-FISH (pH, dissolved oxygen) probes.

2.2. Analysis of spatial distribution of *Macoma calcaria*

An analysis of macrobenthos distribution in the SW part of the Kara Sea has already been presented in earlier publication (Gerasimova et al. 2021). In this paper, we draw our attention to those benthic associations in which *Macoma calcaria* played a substantial role. For their identification the station similarity was assessed as Bray–Curtis index (Clarke & Warwick 2001) in respect of biomass of individual taxa and then the cluster analysis (UPGMA algorithm) and multi-dimensional scaling (MDS) were employed. Prior to the analysis, biomass values were standardized dividing each specific value by the sum biomass at each station. The cluster analysis included all stations of 2012 (No. 001-104) and only 4 stations of 2013 (No. 110–113). As it was pointed in previous paper (Gerasimova et al. 2021) most of the 2013 sampling stations (No. 105–108, 114–119) were excluded from the analysis by several reasons: in 2013 the sampling was mainly confined to shallow-most areas (depths of 4–15 m) and it was not always possible to take equivalent three replicates at the station due to specific features of the sediments (boulders, rocks), besides, several stations (for example, No. 106, 115, 116 and others) were located too far from the main sampling area (see Online Resource 1). Prior to the analysis, all doubtful records of possibly inaccurate or problematic taxa identifications, were reduced to higher taxonomic levels (genus, family or order, etc.). The results of cluster analysis were subjected to the SIMPROF procedure (Clarke et al. 2008), which assess the significance level of the identified groups. As a result, we analyzed only reliably distinguished clusters.

Only those stations, where *Macoma calcaria* were found, were included in further processing. The station similarity in respect of abiotic parameters was assessed using Euclidean distance and then cluster analysis (UPGMA algorithm) and multi-dimensional scaling (MDS) were used to distinguish station groups. The results of the cluster analysis and the ordination were verified by ANOSIM analysis. Simper analysis was employed to estimate the contribution of individual abiotic variables to the differences in station groups. Near-bottom water temperature and oxygen concentration were excluded from this analysis since the 2012 survey lasted too long, for two months (10 August – 16 September, Online Resource 2), so these parameters could change noticeably.

Spearman rank correlation coefficient (at significance level $\alpha \leq 0.05$) was used to estimate the role of the environmental factors in the *Macoma calcaria* distribution.

The contingency analysis of *Macoma calcaria* and some representatives of macrobenthos distribution was conducted only for frequently occurring species (occurrence more than 50% at the stations with *Macoma*) using a cluster analysis, MDS (on the basis of Bray–Curtis index) and correlation analysis (Pearson correlation and Spearman rank correlation coefficients (at significance level $\alpha \leq 0.05$)). The

computation of the Pearson correlation coefficient was carried out using the transformed data (square root).

All calculations were performed using PAST V3 software (Hammer et al. 2001), Statistica v.10, PRIMER V6 (Clarke & Warwick 2001).

2.3. Analysis of mollusc growth heterogeneity

Shell length (L , Online Resource 3) of *Macoma calcaria* was measured to the nearest 0.1 mm with a caliper. Age and growth characteristics of molluscs were mostly determined by analyzing external shell morphology (Online Resource 3).

The bivalve age determination on the basis of external shell morphology is known to be insufficiently accurate (MacDonald & Thomas 1980; Thompson et al. 1980; Murawski et al. 1982; Appeldoorn 1983; Wenne & Klusek 1985; Zolotarev 1989; Cardoso et al. 2013). In particular, the age determination of *Macoma calcaria* from western Greenland by counting external growth rings was extremely troublesome (Petersen 1978). There are many ways to estimate the bivalve age: direct experimental observations, physicochemical methods, studying growth marks on shells or analysis of the bed size structure (Zolotarev 1989). Physicochemical methods relying on estimation of the ratio of oxygen stable isotopes, magnesium and strontium content and radiography of shell have been successfully used in the last decades for the age determination in bivalves (Zolotarev 1989). They were mostly used to confirm the annual character of the inner growth marks of the shell (Zolotarev 1989; Witbaard 1996; Khim 2001; Khim et al. 2003; Ambrose et al. 2006; Kilada et al. 2007; Cardoso et al. 2013). However, these methods are time- and effort-consuming, and so are not practical for processing large amounts of material. Thus the analysis of external shell morphology remains the most common method for the age determination in bivalves (Zolotarev 1989; Scarlato 1990). Some criteria allowing to distinguish additional rings among annual with a greater certainty have been proposed (Pannella & MacClintock 1968; Kennish & Olsson 1975; Taylor & Brand 1975). The possibility of using external shell morphology to determine the age of *M. calcaria* was demonstrated for specimens from the White and Pechora Seas (Lisitsyna et al. 2017; Gerasimova et al. 2019).

Both individual and group (mean) growth characteristics were used to analyze the variability of *Macoma calcaria* growth rate in the study area. Individual growth history of each mollusc (individual age series) was reconstructed by measuring shell length during all annual growth delays (see Online Resource 3). In total, growth rings were measured in 156 specimens. Group growth parameters (mean age series) were calculated for each station by averaging individual growth characteristics.

Growth age series were compared using an algorithm suggested by Maximovich (1989): a pairwise comparison of growth age series and their clustering was carried out using the analysis of residual variances with regard to growth models. Significance of variance distinctions was estimated by Fisher's F-statistic (F). The ratio of Fisher's F-statistic to the critical F value at $p < 0.05$, F/F_{cr} , was used as a measure of distance between the compared age series. $F/F_{cr} < 1$ meant the absence of significant

differences between the compared age series. Clustering was performed using the method of weighed pair-group average. Usually the von Bertalanffy equation is used for approximation of growth age series (Maximovich 1989):

$$L_t = L_\infty (1 - \exp^{-k(t-t_0)})$$

where L_t is the shell length (mm) at time t (year); L_∞ (asymptotic or theoretically maximal length, mm), k (rate at which L_∞ is approached, year^{-1}) and t_0 (theoretical time at which $L_t = 0$, year) are constants.

However, if the age series did not indicate growth slowdown with age, then the von Bertalanffy equation could not be used for their approximation (Maximovich 1989). In these cases, for cluster analysis the age series were approximated by the linear equation:

$$L_t = a + bt$$

- where a and b are constants.

In this paper the von Bertalanffy equation was used only for *Macoma calcaria* ontogenetic growth reconstruction.

Since the reliability of age determination of *Macoma calcaria* by the external shell morphology has been subjected to quite justified doubts (Petersen 1978), additional attempts have been made to estimate the mollusc age by internal growth marks at the shell cross-sections (Fig. 1). The annual nature of internal growth marks in this species was confirmed by the isotope method (Khim et al. 2003). To make the shell cross-sections the right valves of the shells were embedded into epoxy resin (to avoid crumbling or breaking when cutting). After that the shells were sawn from the top to the outermost edge using a precision cutting machine with a low cutting speed DTQ-5. Then the shell cross-sections were grinded (using MP-2 grinding machine) and polished. The growth marks at the hinge teeth sections in umbo area were counted under a binocular microscope. Totally shells of 23 specimens were processed in such a way.

3. Results

Cluster analysis and SIMPROF procedure ($p < 0.05$) allowed dividing all stations into 17 clusters based on taxa biomass values (Online Resource 4) (Gerasimova et al. 2021). The resulting groups, as a rule, were formed in accordance with the taxa dominating by biomass. We considered all the identified clusters as separate macrobenthic communities (Online Resource 5).

In one of the identified communities (cluster 8) *Macoma calcaria* dominated by biomass (27% of the total benthos biomass), and in two others (clusters 9 and 15) they were subdominant species (12 and 20% of the total biomass respectively) (Fig. 2). Macrobenthos characteristics and some abiotic

parameters in the clusters are presented in Table 1. These communities were found at depths of 30–50 m, mainly on silty sediments (the proportion of silt in the sediments was about 80% and more).

Table 1

Some macrobenthos characteristics and accompanying abiotic conditions in the clusters, in which *Macoma calcaria* dominated (or subdominated) by biomass.

Characteristics	Clusters		
	8	9	15
Total species	95	114	69
Total density (Average \pm SE, ind. m ⁻²)	16.7 \pm 1.6	22.78 \pm 1.37	23.32 \pm 1.12
Total biomass (Average \pm SE, g m ⁻²)	3.82 \pm 1.19	6.56 \pm 0.77	8.14 \pm 0.94
Taxa dominating by biomass	<i>Macoma calcaria</i>	<i>Astarte</i> sp.	<i>Serripes groenlandicus</i>
Density of <i>Macoma calcaria</i> (Average \pm SE, ind. m ⁻²)	40 \pm 13	36.67 \pm 10.44	35.6 \pm 7.75
Biomass of <i>Macoma calcaria</i> (Average \pm SE, g m ⁻²)	26.2 \pm 5.33	25.58 \pm 5.18	31 \pm 5.1
Depth, m (min-max)	30–53	30–42	19–30
Silt proportion in sediments, % (min-max)	82–93	37–97	72–97

Cluster number as on Fig. 3.

3.1. Distribution of *Macoma calcaria* in the SW part of the Kara Sea

Macoma calcaria were found at 37 stations out of 119 at depths of 4 to 190 m (Fig. 3, Table 2). Silt (particles less than 0.1 mm) and fine sand (particles 0.25 – 0.1 mm) predominated in the sediments at these stations (about 80% and 20% in average, correspondingly). The near-bottom water temperature varied from – 1.6 to 6.4°C, and the salinity – from 30.6 to 33.8.

Table 2
Average characteristics of sediments and near bottom waters and their range (R) (*Min-Max*) at stations, where *Macoma calcaria* were met.

Characteristics	Average ± SE	R
Depth (m)	-	4-190
Pebble > 10 mm	0.03 ± 0.01	0-0.3
Gravel 10 - 1 mm	0.2 ± 0.03	0-0.9
Coarse sand 1-0.5 mm	0.15 ± 0.05	0-1.3
Medium sand 0.5 - 0.25 mm	1.3 ± 0.45	0-12.6
Fine sand 0.25 - 0.1 mm	19.9 ± 3.44	1.6-81.8
Silt 0.1-0.005 mm	77.9 ± 3.78	5.3-97.3
Clay < 0.005 mm	0.5 ± 0.17	0-4.9
Temp. (°C)	1.2 ± 0.45	-1.6+6.8
Salinity	32.8 ± 0.16	30.6-34.4
Oxygen (ml l ⁻¹)	7.5 ± 0.09	6.1-8.4
pH	8.1 ± 0.01	7.9-8.3
<i>SE</i> - standard error		

The average density and biomass of *Macoma calcaria* at the stations where they were present were 22 ± 4.6 ind. m⁻² (from 3.3 to 120 ind. m⁻²) and 17 ± 3.3 g m⁻² (from 0.03 to 86.2 g m⁻²) respectively. Density value errors varied at stations from 4 to 100%, and for only 10 stations were less than 50%. The greatest *Macoma* density and biomass were recorded at a depth of 42.5 m on silt sediments (St. 103) where these molluscs were prevalent (Fig. 3). In general, *M. calcaria* dominated by biomass at 11 stations, accounting for 16-44% of the total macrobenthos biomass.

Macoma calcaria were most abundant at depths 19-53 m (density 3-120 ind. m⁻², biomass 0.03-86 g m⁻²), while both in shallower and deeper places they were scarce. The stations where *M. calcaria* were numerous (28 stations in total) were used to study their distribution. There were no statistically significant correlation between *Macoma* abundance and environmental parameters.

The station similarity analysis (cluster analysis and MDS) in respect of abiotic parameters showed (Fig. 4) that there were two significantly different groups of stations (ANOSIM analysis, $p < 0.05$). The main contribution to the differences of these clusters (85%, SIMPER analysis) was made by sediment fractions of silt and fine sand (Fig. 4A).

The density of *Macoma calcaria* on silty sediments (cluster 1) was almost 8 times higher than on sandy sediments (differences are statistically significant, according Mann-Whitney test), and the biomass was almost 2 times higher on silty sediments than on sandy ones (the differences are not statistically significant, Mann-Whitney test) (Table 3).

Table 3
Density and biomass of *Macoma calcaria* in the clusters
(numbers of clusters according to Fig. 4)

Characteristics	Cluster 1	Cluster 2
Density (Average \pm SE, ind. m ⁻²)	30 \pm 6	4 \pm 1
Biomass (Average \pm SE, g m ⁻²)	22 \pm 4	14 \pm 5

Similar results were obtained by dividing stations into two groups on the basis of *Macoma calcaria* dominance by biomass and following analysis of differences in abiotic parameters. As before, the main difference between the distinguished associations was due to fractions of fine sand and silt. At the stations where *Macoma* dominated, the silt proportion was the largest – 85% on average.

To assess the influence of interspecific interactions on *Macoma calcaria* distribution the contingency analysis of frequently occurring taxa and *Macoma* in terms of relative density and biomass at depths of 19–53 m was carried out using cluster analysis and MDS (Fig. 5). A total of 11 such taxa (with taxonomic rank not higher than genus) have been identified. In terms of density *Macoma* showed similar distribution only with sipuncules *Golfingia sp.* and polychaetes *Maldane sarsi* (similarity level about 50%), in terms of biomass - with closely related species *Macoma moesta* (similarity level above 60%) (Fig. 5). Similar results were obtained using correlation analysis, though statistically significant correlation between *M. calcaria* and other taxa were not higher than 0.6 (Table 4).

Table 4
Statistically significant correlation coefficients
(Pearson correlation, r , and Spearman rank
correlation, r_s , (at significance level $\alpha \leq 0.05$))
between *Macoma calcaria* и other taxa based on
density (N) and biomass (B).

Taxon	N		B	
	r	r_s	r	r_s
<i>Maldane sarsi</i>	0.40	-	-	-
<i>Macoma moesta</i>	0.40	-	0.56	0.57
<i>Astarte sp.</i>	-	-0.40	-	-

3.2. Growth of *Macoma calcarea* in the SW part of the Kara Sea

3.2.1. Individual growth

As it was already noted, in total, external growth rings were measured in 156 individuals. The maximum registered shell length and age of *Macoma calcarea* were 37 mm and 20 years, respectively.

To study the individual growth variability, molluscs with well-discernible growth rings were selected. The main difficulty was determination of correct number of growth rings and, accordingly, the exact age of *Macoma calcarea*. In most analyzed specimens only the first four to five growth rings were well-discernible while later rings could be detected with much lesser certainty. In total, 25 specimens of *M. calcarea* were selected for the analysis of individual growth variability. Differences in individual growth rate were substantial - the size of the fifth growth ring varied from almost 4 to 8 mm. The growth rate did not slow down with age and by this reason only the linear equation could be used for approximation of individual age series. Using cluster analysis, 2 groups of individuals with significantly different growth patterns were identified (Online Resource 6). However, the differences in the growth rates between the groups were not large (Fig. 6). Most of individuals belonged to the relatively slow-growing (5 mm in 5 years) group (Makarevich & Druzhkova) (Fig. 6, Online Resource 6). Only three specimens formed a group of relatively fast-growing (7 mm over 5 years) molluscs (Makarevich & Druzhkova).

The distinctions between individual and group growth models were manifested rather early, at the stage of the second to third growth ring (Fig. 6), and persisted afterwards. Cases of compensatory growth (an increase of the growth rate after a period of slow growth) were very rare. There was a positive correlation between the size of the second and the third growth rings (Spearman's rank correlation, $r_s = 0.59$, $n = 25$, $p < 0.05$).

3.2.2. Individual growth

Mean age series could be constructed only for ten stations (No. 47, 49, 53, 54, 72, 74, 79, 94, 98, 103), which were used for the assessment of *Macoma calcarea* group growth variability in the study area. Each mean age series included the mean size of the molluscs at the stage of the first 10 growth rings (Fig. 7A). Group growth variation was less pronounced than individual growth variation. The average size of the 5th growth ring varied between stations less than 1.5 times, from 4.9 to 6.4 mm. There were no significant differences between stations in terms of *M. calcarea* group growth (Online Resource 7), despite wide variation in abiotic conditions: depths varied from 20 to 53 m, the proportion of silt in the sediments changed from 66 to 93%, etc. Therefore, a joint model of *Macoma* growth in the study area was constructed by averaging all individual sizes of growth rings at each age (Fig. 7B). The molluscs had a

very low growth rate in the first 4 years of life (less than 2 mm per year), and during the next 5–13 years growth rate was about 2 mm per year.

Since the age determination of *Macoma calcarea* by the external shell morphology is often problematic, attempts were made to additionally estimate their age by the internal growth marks using shell cross-sections. Comparison of the results obtained for the external growth rings and inner growth marks showed that age determination by both methods is quite similar, the inner marks almost completely double the outer rings (Fig. 8). Thus in case of heavily eroded shells, the analysis of cross-sections is a way to relatively secure determine the mollusc age. Overall, the internal marks are more distinguishable and easier to count than external ones. The age determination by internal marks showed the maximum age of *Macoma* in the Kara Sea was 21 years.

Information on the growth pattern of molluscs obtained by different methods complements each other well. As a result, it was possible to construct an ontogenetic model of *Macoma calcarea* group growth within the studied water area (Fig. 8). The average annual growth rate of molluscs for the entire life cycle (for 20 years) was about 2 mm per year.

4. Discussion

The studies of the Kara Sea benthic biota has been going on for over 100 years (Filatova & Zenkevich 1957; Zenkevich 1963; Antipova & Semenov 1989; Kiyko & Pogrebov 1997; Galkin 1998; Jørgensen et al. 1999; Denisenko et al. 2003; Deubel et al. 2003; Kulakov et al. 2004; Kozlovskiy et al. 2011; Vedenin et al. 2015; Azovsky & Kokarev 2019; Gerasimova et al. 2021). They showed that bivalve molluscs *Macoma calcarea* have been a steady component of relatively shallow (mostly down to 50 m) benthic communities of this Sea for many decades (Zenkevich 1963; Antipova & Semenov 1989; Kiyko & Pogrebov 1997; Denisenko et al. 2003; Kulakov et al. 2004; Vedenin et al. 2015). The communities which we distinguish in the southwestern part of the Kara Sea via the analysis of 2012–2013 data, where *M. calcarea* dominated or subdominated, have appeared to be very similar (in terms of biological traits, location and environment conditions) to those registered by previous researchers (Antipova & Semenov 1989; Kiyko & Pogrebov 1997; Kulakov et al. 2004).

4.1. Distribution patterns of *Macoma calcarea* in the SW Kara Sea

Until now, the information on the *Macoma calcarea* distribution in the Kara Sea was practically absent. Generally, *Macoma* density and biomass (average and maximum), vertical distribution, the preferred environmental conditions (sediments, temperature and salinity), which we observed in the SW Kara Sea, were similar to those in other parts of the species range (Deryugin 1928; Zachs 1929; Guryanova 1948;

Ushakov 1953; Evseev 1981; Fedyakov 1986; Kamenev et al. 2004; Naumov 2006; Britaev et al. 2010; Gerasimova et al. 2019; Noskovich 2020, 2021). The only exception was the southern part of Chukchi Sea with depths less than 100 m, where *M. calcaria* formed dense aggregations with density and biomass of more than 6000 ind. m⁻² and about 4 kg m⁻², respectively (Sirenko & Gagaev 2007).

The revealed differences in *Macoma* preferred depths and, accordingly, environmental conditions in the Kara and Pechora Seas are of particular interest. According to our data, *Macoma calcaria* in the SW Kara Sea are mainly concentrated at depths of 20–50 m while the whole range is 4 to 190 m. At the Pechora Sea, the species was found at depths down to 50 m, while their densest beds were confined to a shallower zone - less than 20 m (Gerasimova et al. 2019). An attempt to explain these differences in the vertical distribution by the biogeographic affiliation and by features of reproductive ecology was not successful. *M. calcaria* belong to the Boreal-Arctic species, which optimal temperatures for life and reproduction are in the range from - 2°C to + 6–10°C and from - 1°C to + 3–6°C, respectively (Scarlato 1981). This can probably explain the relative scarcity of *Macoma* in the SW Kara Sea at depths of more than 40–50 m. The local summer warming, as a rule, affect the waters at depths down to 30 m, and at a maximum (in some years) - down to 60–70 m (Mokievsky 2016). At greater depths, the near-bottom temperature is less than - 1°C throughout the year. In the Pechora Sea, summer warming (up to + 8 °C) was recorded down to a depth of 15–18 m, while negative values during the warm period were observed only deeper than 50 m (down to -1°C) (Zalogin & Kosarev 1999). The differences in *Macoma* vertical distribution in these Seas could probably be the sequence of inter-population differences. The development of *M. calcaria* presumably occurs with metamorphosis and pelagic larva, though, judging by the egg size (175–200 microns), the duration of the pelagic stage should not be long (Oertzen 1972; Naumov 2006; Noskovich 2021). The adaptation of the populations to a specific environment could lead to a shift in optimal temperatures including for reproduction. Populations from the Pechora and Kara Seas may belong to different ecotypes (Odum 1986). At this point, all of the above is purely hypothetical. The study of *Macoma* population structure in the northern seas may become the subject of future research, including molecular genetic ones.

At this stage of the study, we were only able to associate the distribution of *Macoma calcaria* within the preferred depth range (20–50 m) at the SW Kara Sea with the characteristics of the bottom sediments. *Macoma* abundance in the study area tended to increase on silty sediments. This is probably connected with their feeding type. *M. calcaria* is predominantly deposit-feeder (Naumov 2006). The average grain size of sediments usually reflects the amount of detritus. Some researchers explained the presence of dense *Macoma* beds in the southern Chukchi Sea by favorable feeding conditions (Sirenko & Gagaev 2007). However, in our studies *M. calcaria* abundance did not always correlate with the sediment type. At some stations with silty sediments *Macoma* was missing or only a few individuals were met.

It should be noted that *Macoma calcaria* is not an obligate deposit-feeder. It can also switch to suspension-feeding (Naumov 2006), which could affect the choice of biotope. Due to a relatively low density of this species (as rule, less than 100 ind. m⁻²), three grab samples per station can hardly be considered as reliable amount for correct abundance estimation. The standard error of abundance

estimation varied in our studies from 4 to 100%, and only for 10 stations it was less than 50%. The Agassiz trawl is preferable for sampling in such cases (Gerasimova & Maximovich 2013; Shulgina et al. 2015).

Sometimes *Macoma calcarea* distribution could be not quite consistent with their ecological traits. *M. calcarea* bed structure in the northern seas is known to be unstable, which results in long-term changes in their density and biomass (Petersen 1978; Gerasimova & Maximovich 2013; Lisitsyna et al. 2017). This complicates the analysis of their distribution based on a case study without taking into consideration the long-term bed dynamics.

Analysis of effect of interspecific interactions on the distribution of *Macoma calcarea*, showed that *Macoma* density distribution was similar to that of sipuncules *Golfingia sp.* and polychaetes *Maldane sarsi*, and in relation to biomass - to the closely related species *Macoma moesta*. This is probably not the result of species interaction, but of similar environmental preferences. All the above-mentioned species are deposit-feeders and prefer silty biotopes. Their biogeographic characteristics are also similar - they belong to Boreal-Arctic fauna (Scarlato 1981; Jirkov 2001; Zhuravleva 2010). The weak negative correlation between the abundance of *Macoma* and *Astarte sp.* can be explained by different feeding types of these species (deposit-feeder and seston-feeder, respectively) (Scarlato 1987).

4.2. The growth heterogeneity of *Macoma calcarea* in the SW part of Kara Sea

One of the most substantial results in this study was the demonstration of the possibility of using the external shell morphology for *Macoma calcarea* age determination. As shown in "Results", the results of age determination in these molluscs by external and internal growth marks practically did not differ. However, for specimen of older ages and with strongly eroded shells, age determination using shell cross-section is still preferable.

The maximum shell length and longevity of *Macoma calcarea* in the SW Kara Sea (37 mm and 21 years, respectively), in general, fit well with the known range of these characteristics in different geographic locations. According to literature data, the maximum shell length of *M. calcarea* varied within the species range from 22 to 70 mm, while the life span ranged from 9 to 26 years (Petersen 1978; Antipova 1979; Selin 2010; Lisitsyna et al. 2017; Noskovich 2021). The largest representatives of this species, usually 25–45 mm, are known from the Far East Seas, while an individual with a shell length of 70 mm was found in the Tatar Strait of the Sea of Japan (Scarlato 1981). *Macoma* caught off the northeast coast of Sakhalin, 51.5 mm in size, was 18 years old (Selin 2010), however, this age determination cause a certain doubts, since only dead shells were used in the studies, and the tabular data in the article did not correspond the figure.

The average annual growth rate of *Macoma calcarea* throughout its life cycle in the SW Kara Sea (about 2 mm per year) was very close to that recorded in the coastal waters of West Greenland (depths 3-107 m) (Petersen 1978), in the Pechora Sea (depths from 8 to 52, 5 m) (Gerasimova et al. 2019), in the coastal

waters of the Novaya Zemlya archipelago (depths 60–203 m) (Noskovich 2021), (Fig. 9). *M. calcarea* in the Kara Sea as well as in the Pechora Sea had an extremely slow growth rate in the first years of life (Fig. 9). The average size of the first growth ring was about 1 mm, of the second – 1.6 mm and 3-years old molluscs had the shell length of 3–4 mm. Perhaps the reasons for such a low growth rate are related to severe temperature conditions of the Kara Sea, which is covered with ice from September-October to the end of June - early July (Gerasimov 1970; Pavlov & Pfirman 1995) and as a result, is very low productive (Berger 2007). Unlike the Kara Sea, the White Sea, where *M. calcarea* grew much faster in the first years of life (Fig. 9), is free of ice by the end of May (Babkov & Golikov 1984) and much more productive (Berger 2007).

Our results showed that there were no significant differences in *Macoma* group growth in different parts of the study area, despite the noticeable differences in environment conditions (depths, sediments, etc.). The variability of *Macoma calcarea* individual growth was also relatively weak. Similar results were obtained earlier for specimens from the White Sea (Lisitsyna et al. 2017), the Pechora Sea (Gerasimova et al. 2019) and from West Greenland (Petersen 1978). A poor variability of *M. calcarea* group growth was probably due to optimal for *Macoma* environment conditions within the study area. A comparative analysis of *M. calcarea* growth was carried out only for the stations with a relatively high abundance of this species. According to the Optimum Principle, the densest beds of the species are formed under the most favorable conditions. The characteristics of the habitats under consideration might optimal for this species. The bivalves are known to have the highest growth rate in such habitats. Thus, the absence of significant differences in *M. calcarea* growth patterns at separate stations could reflect the uniformity of habitats in terms of optimal condition. It should also be noted that average abundance of *M. calcarea* at the most analyzed stations was relatively similar, 43–120 ind. m⁻².

Variation of *Macoma calcarea* individual growth within the study area was more pronounced than variation of the group growth, but was still generally low. Variation of *M. calcarea* individual growth was previously studied only in the White and the Pechora Seas (Lisitsyna et al. 2017; Gerasimova et al. 2019). In these papers, the differences of *Macoma* growth characteristics were associated only with the features of the initial growth period of molluscs. A statistically significant positive correlation was found between the growth rate during the first year of life and the size of the first growth ring (Lisitsyna et al. 2017), and between the growth rate during the third year of life and the size of the second growth ring (Gerasimova et al. 2019). Similar results were also obtained in the present study. The differentiation of the individual growth rates of *M. calcarea*, apparently, occurred early in the life cycle and persisted afterwards. Cases of compensatory growth were infrequent.

Mechanisms responsible for different growth patterns of bivalves are poorly studied. The differences in molluscan growth at the early stages can be associated with the conditions of spat formation. The correlation between the size by the start of the second growth season and later growth rate during the entire life cycle was shown for several bivalves such as *Mytilus edulis* (Gerasimova et al. 2014), *Mytilus trossulus* (Gagaev et al. 1994), *Macoma balthica* (Cloern & Nichols 1978), *Macoma incongrua* (Maximovich & Lysenko 1986), *Mya arenaria* (Gerasimova et al. 2016; Gerasimova et al. 2017) and

Macoma calcaria (Lisitsyna et al. 2017). In *M. calcaria* the differences in size by the start of the second growth season could be connected with the time of juvenile settling due to prolonged (up to 2–4 months) reproduction period in the northern seas (Ockelmann 1958; Petersen 1978; Günther & Fedyaikov 2000). As it was shown for *Mya arenaria* in the White Sea (Gerasimova et al. 2021) and *M. balthica* in the estuary of the Gironde River (southwestern France) (Bachelet 1980), by the time of the first growth delay, the shell length of the molluscs varied almost 5-fold due to a prolonged spawning period. For several bivalves at the White Sea an almost linear dependence of the growth rate on the size of their first growth ring was identified (Gerasimova et al. 2003; Gerasimova et al. 2014; Gerasimova et al. 2017; Gerasimova et al. 2021). Accordingly it can be assumed that specimens that have reached a larger size before the first winter will grow faster afterwards. We could not assess the dependence of the mollusc growth rate on the size of the first growth ring due to erosion of the shell umbo area, but significant linear correlation between the *Macoma* growth rate during the third year of life and the size of the second growth ring was found (Spearman rank correlation coefficient was 0.6).

5. Conclusion

Macoma calcaria were for a long time (at least for the last 100 years) a characteristic component of coastal benthic associations in the southwestern part of the Kara Sea, and sometimes dominated by biomass at depths less than 50 m. We were able to relate the distribution of *M. calcaria* in study area within 20–50 m depths only to the characteristics of the bottom sediments. Trends in *M. calcaria* distribution quite logically corresponded to their feeding type. The *M. calcaria* density and biomass was, accordingly, 8 and 2 times higher on silty sediments than on sandy ones. There was no obvious effect of interspecific relationships on the *M. calcaria* distribution.

The possibility is shown to use the external shell morphology of *Macoma calcaria* for their age determination. The results of age assessment based on external and internal growth marks practically did not differ. However, for older individuals or those with heavily eroded shells, age determination using shell cuts is still preferable. The maximum life span and shell length of *M. calcaria* in the SW Kara Sea were 21 years and 37 mm, respectively. Average annual growth rate was about 2 mm per year. The characteristics of *M. calcaria* group growth were very similar in different habitats of SW Kara Sea and in different parts of their range. The variability of individual growth was also relatively poor. The *M. calcaria* individual growth rate was to a great extent determined by the characteristics of the initial period of molluscan growth.

Declarations

Compliance with Ethical Standards

No potential conflict of interest was reported by the authors.

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CRediT author statement

Kseniya N. Lisitsyna: Investigation, Data Curation, Formal analysis, Writing - Original Draft, Visualization, Alexandra V. Gerasimova: Conceptualization, Methodology, Writing - Review & Editing.

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ELECTRONIC SUPPLEMENTARY MATERIAL

Online Resource 1. Sampling stations in the Kara Sea: 1–104 – stations in 2012, 105–119 – stations in 2013 (Gerasimova et al. 2021).

Online Resource 2. Sampling time, coordinates, depth, sediment structure, bottom-water temperature, salinity, oxygen level and pH at each station (Gerasimova et al. 2021).

Online Resource 3. Photo and scheme of measurements of *Macoma calcaria*. *L* – shell length; Growth rings are shown by arrows and numbers (3-6).

Online Resource 4. Dendrogram showing station grouping based on a cluster analysis of taxon biomass values (Bray–Curtis similarity). 1-17 – clusters (Gerasimova et al. 2021).

Online Resource 5. Benthic communities’ distribution in the study area in 2012-2013. The cluster names are as in Online Resource 4 (Gerasimova et al. 2021).

Online Resource 6. Similarity dendrograms of individual age series of *Macoma calcaria*. Y axis - ratio F/Fcr (see Materials and Methods for explanation); X axis - station number_individual age series number; 1, 2 - clusters

Online Resource 7. Similarity dendrograms of mean growth of *Macoma calcaria* at the stations. Y axis – ratio F/Fcr; X axis – station number

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Figures

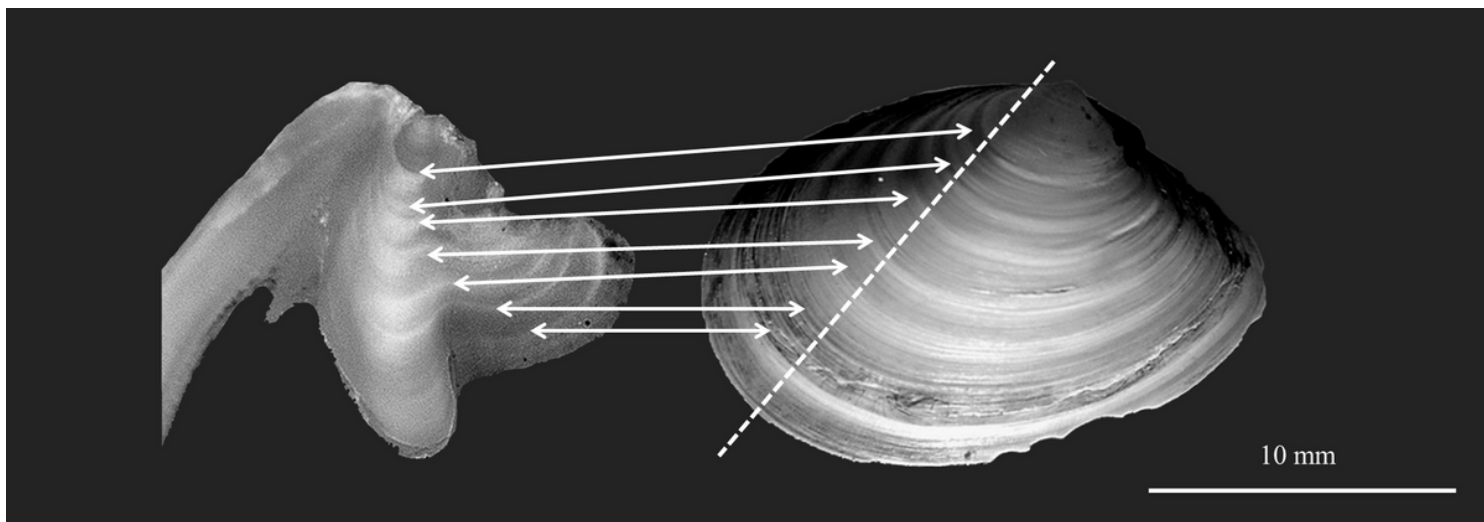


Figure 1

Determination of *Macoma calcaria* age by shell cross-sections. The specimen is 10 years old, the shell length is 19 mm; the dotted line on the left figure shows the direction of the shell cut; the arrows show the correspondence of the rings on the section and on the shell outer surface; 10 lines can be distinguished on the cross-section.

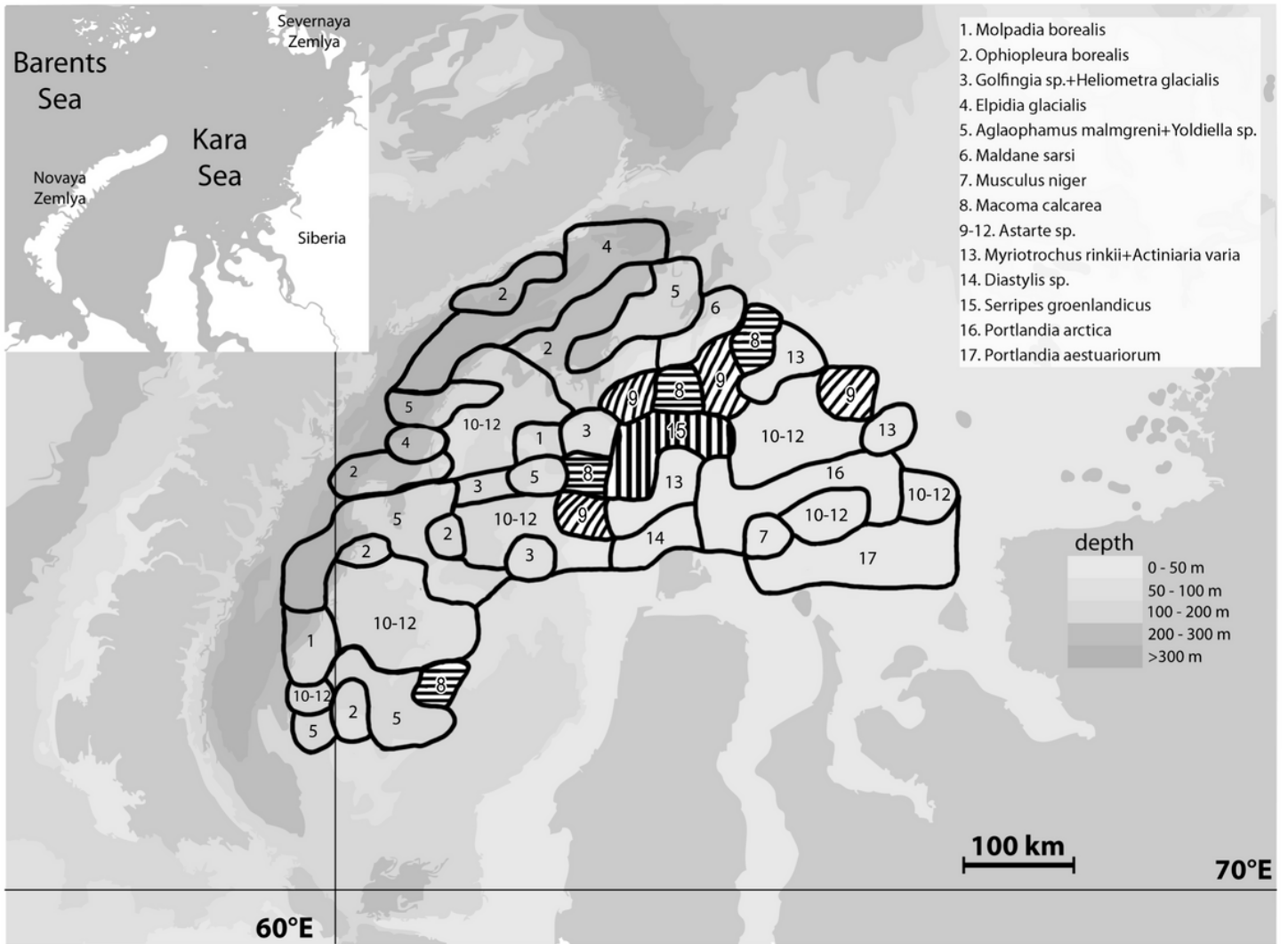


Figure 2

Distribution of benthic communities where *Macoma calcarea* dominated (or subdominated) by biomass. The cluster names are the same as in Online Resource 4.

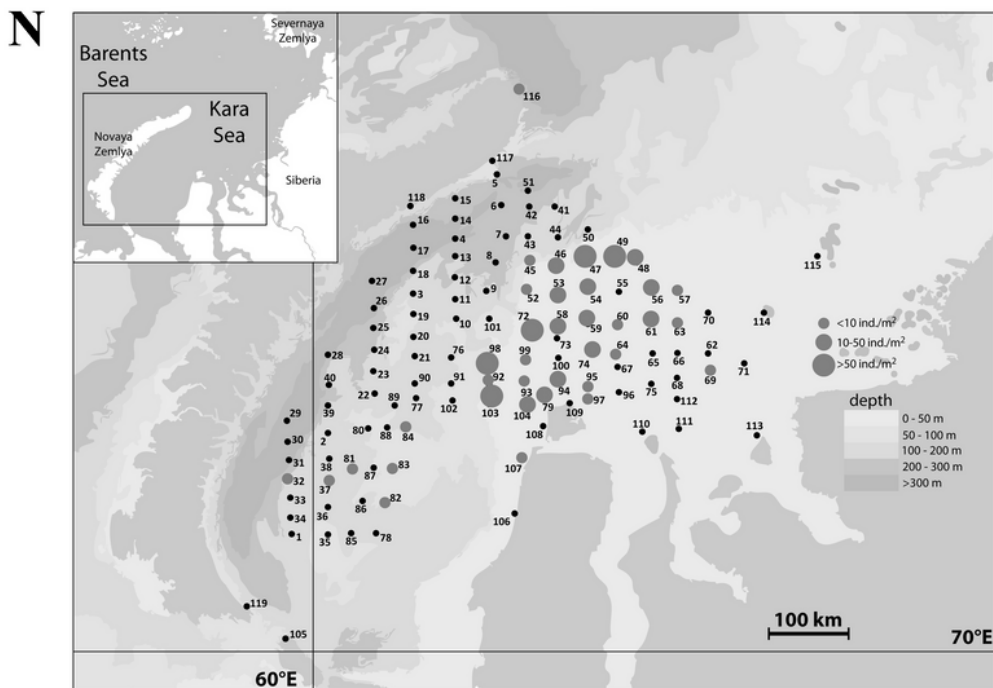
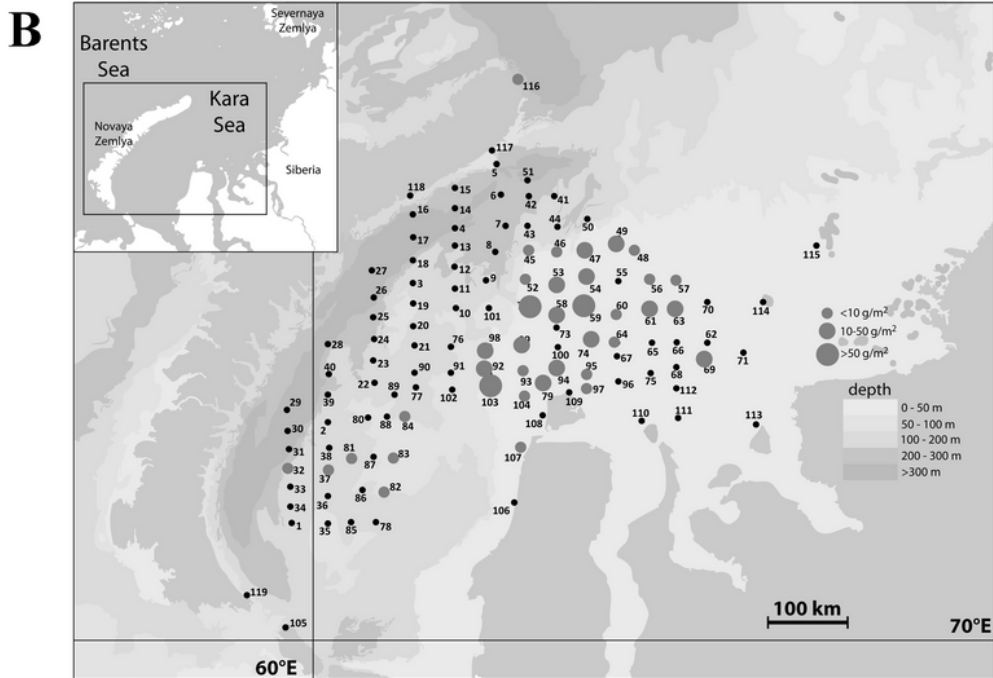


Figure 3

Biomass (B, g m^{-2}) and density (N, ind. m^{-2}) of *Macoma calcarea* at the stations.

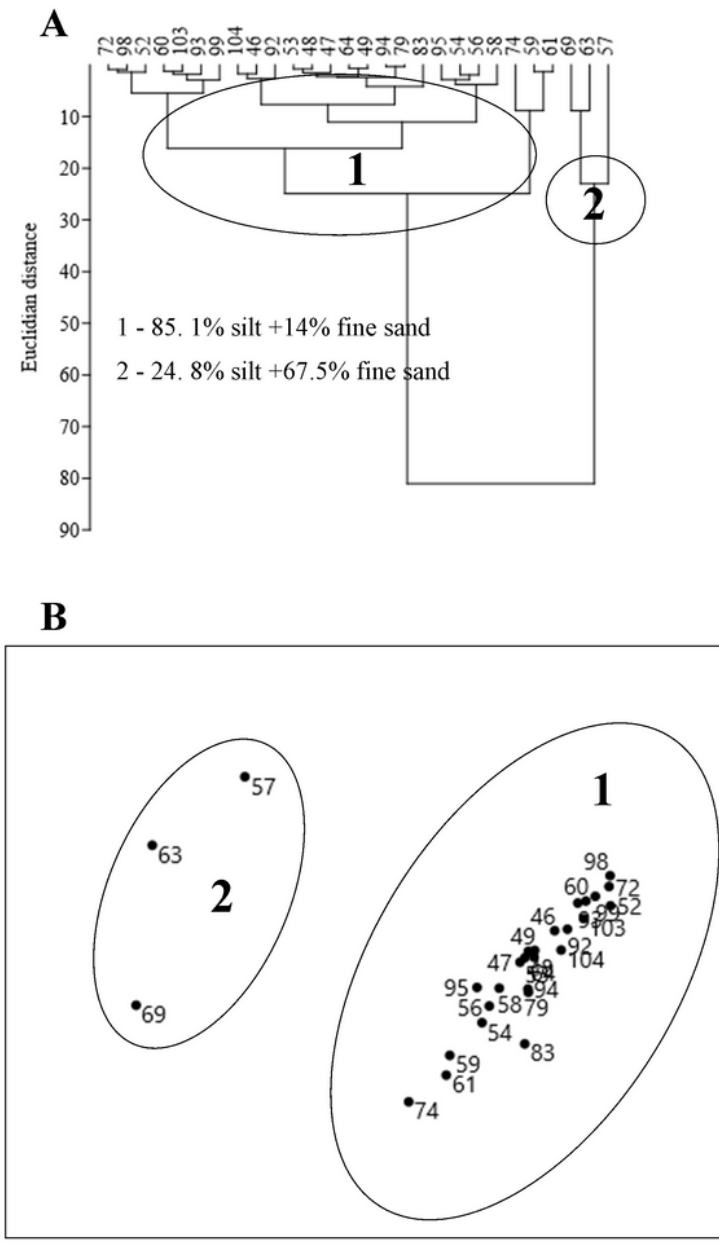


Figure 4

Grouping of the stations based on a cluster analysis (A) and multi-dimensional scaling (B) of environmental data. 1 and 2—clusters

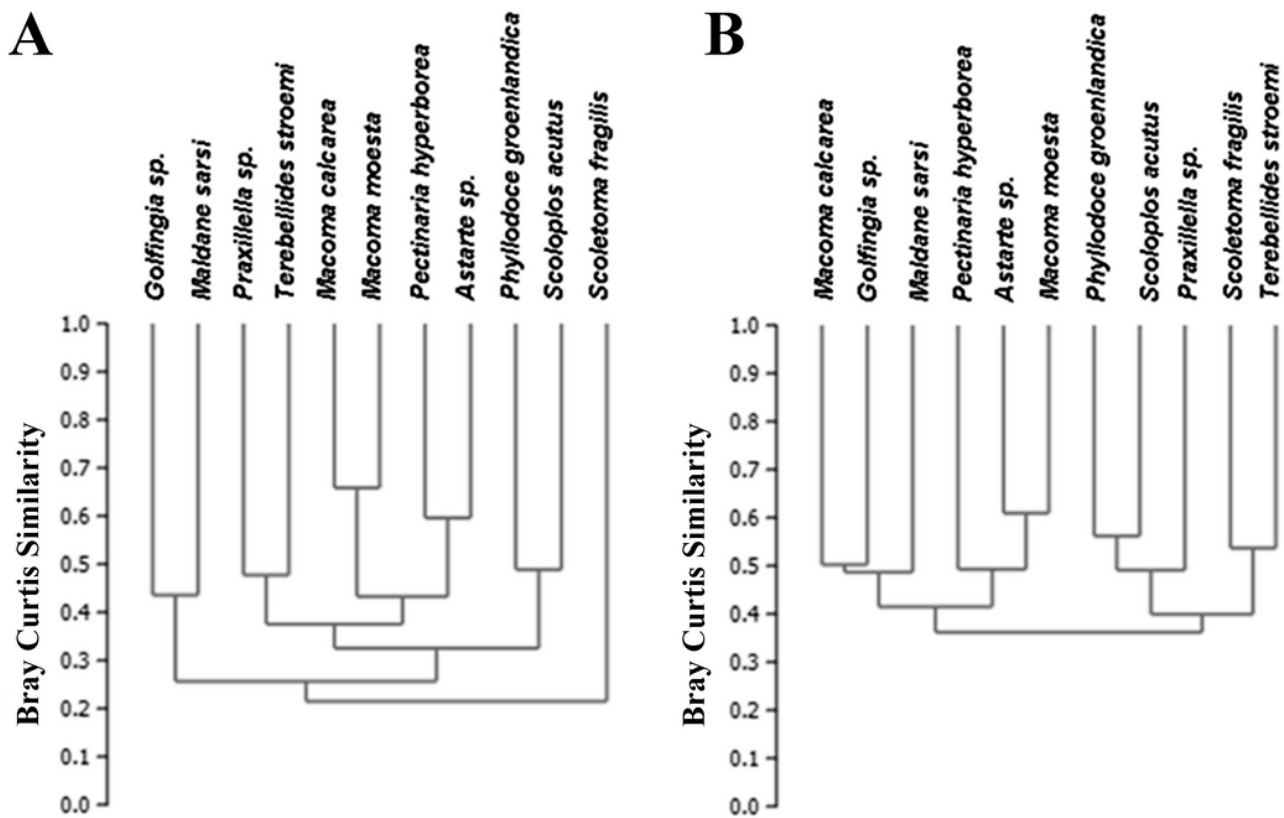


Figure 5

Similarity in the distribution of frequently occurring taxa and *Macoma calcarea* based on biomass (A) and density (B) values.

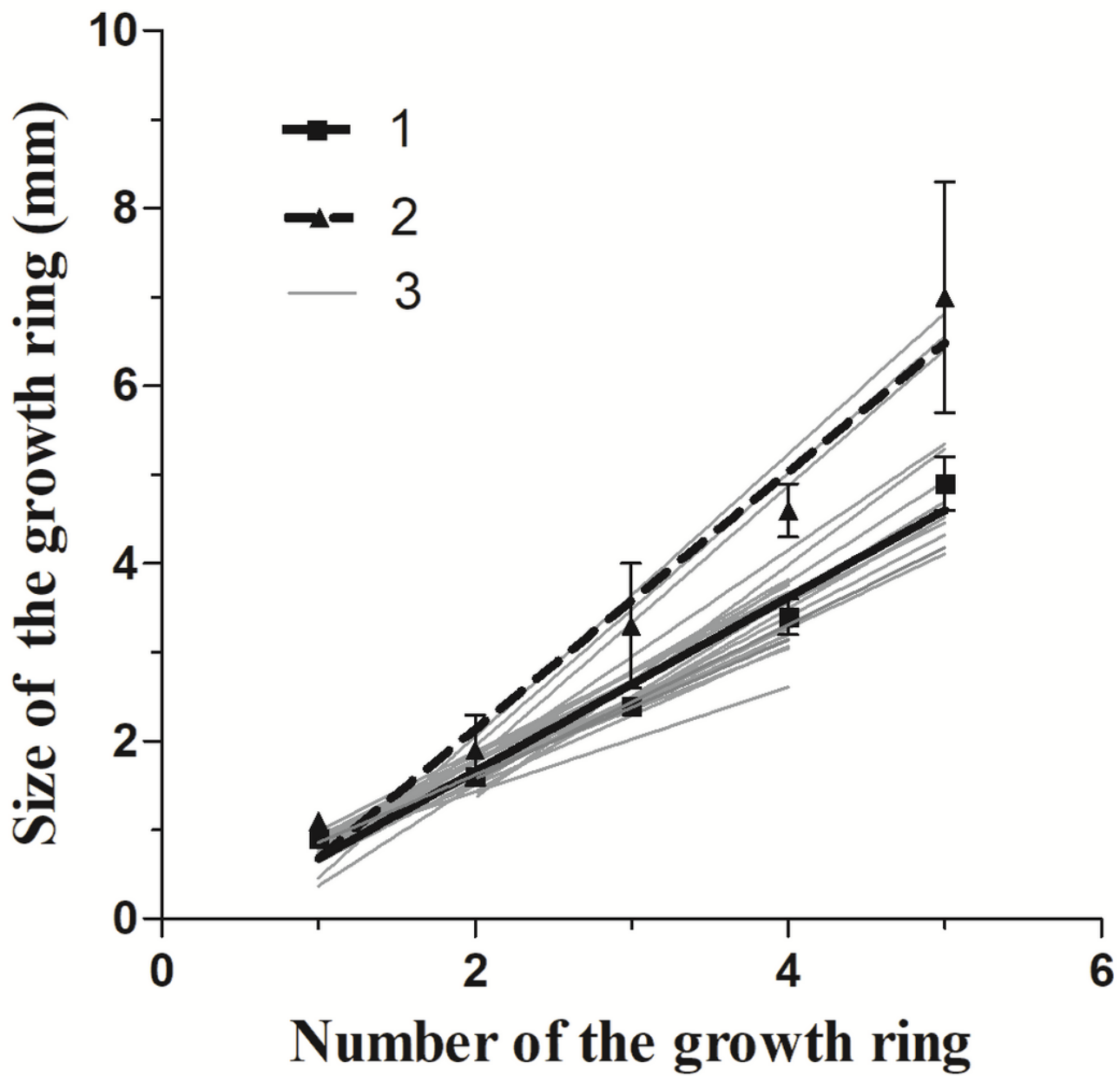


Figure 6

Individual growth lines (3) and mean growth of *Macoma calcarea* in the clusters 1, 2 (Online Resource 6). Dots - average sizes of growth rings; vertical lines indicate 95 % confidential intervals.

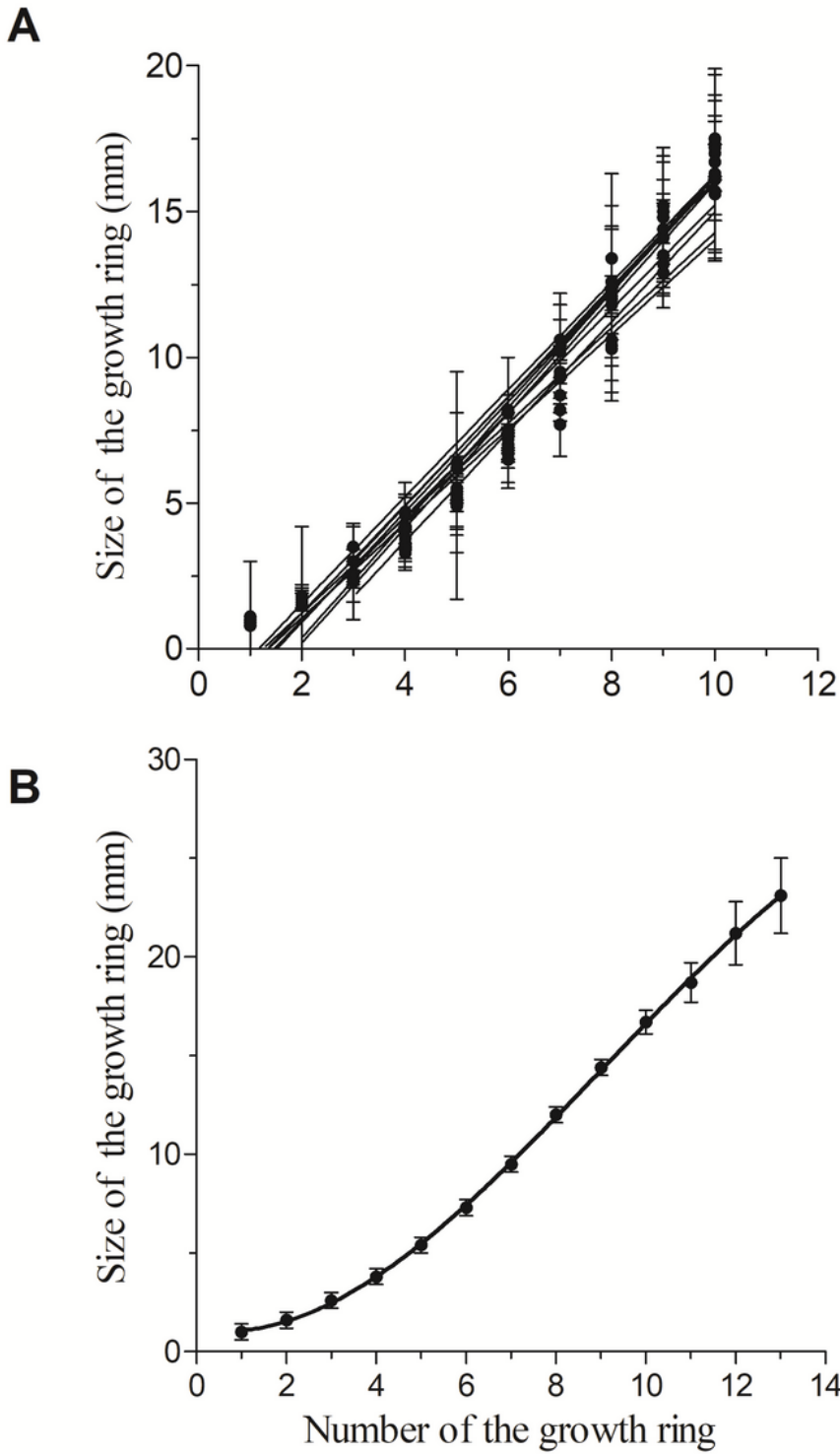


Figure 7

Mean growth of *Macoma calcaria* at separate stations (A) and in the studied area (B). A - each line is a reconstruction of group growth at each station (Online Resource 7). Dots are the average sizes of the growth rings; vertical lines are 95% confidence intervals

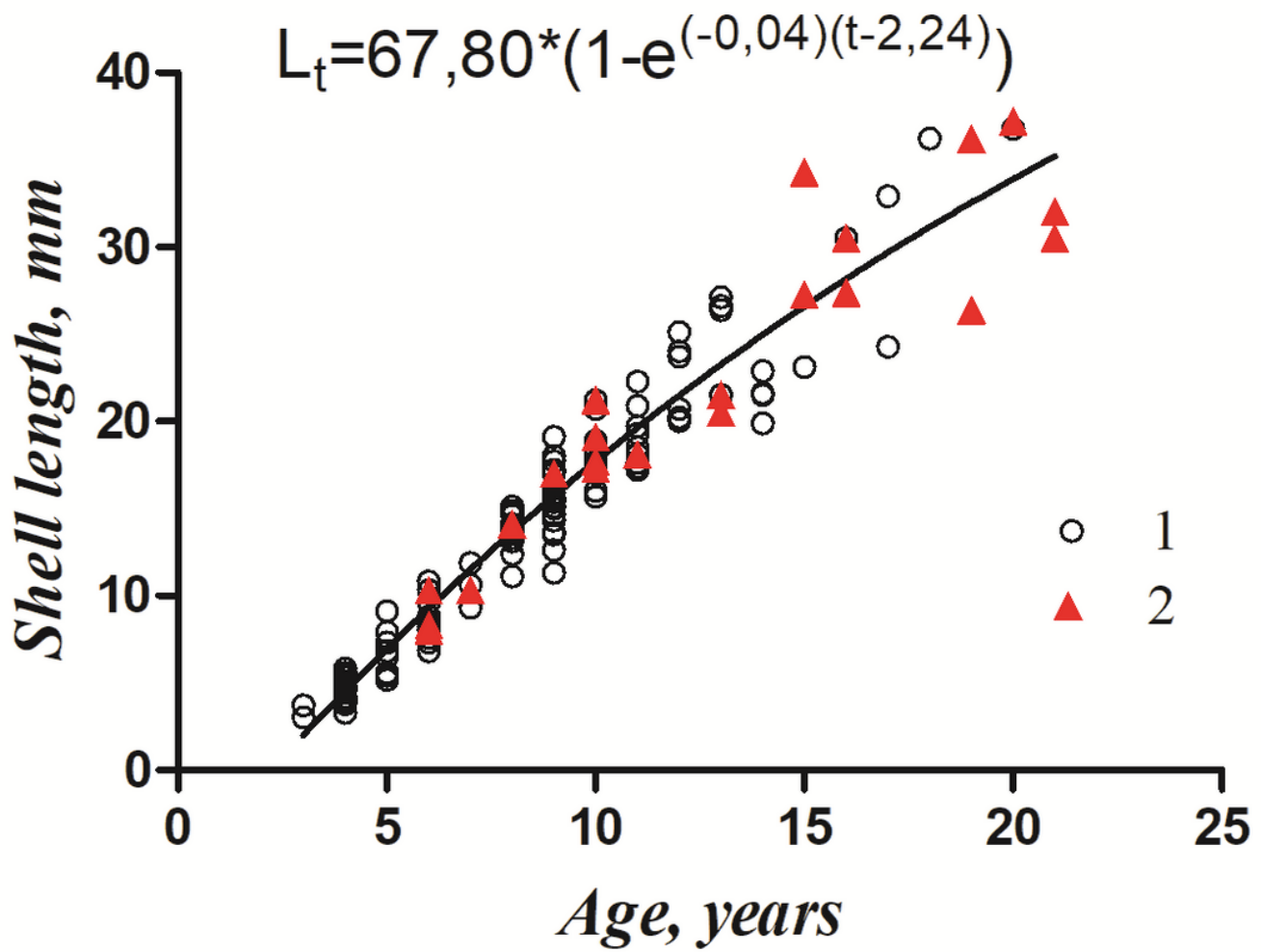


Figure 8

Comparison of the results of determination of the age of *Macoma calcarea* in the Kara Sea, assessed by both the external growth rings and growth marks at the shell cross-sections.

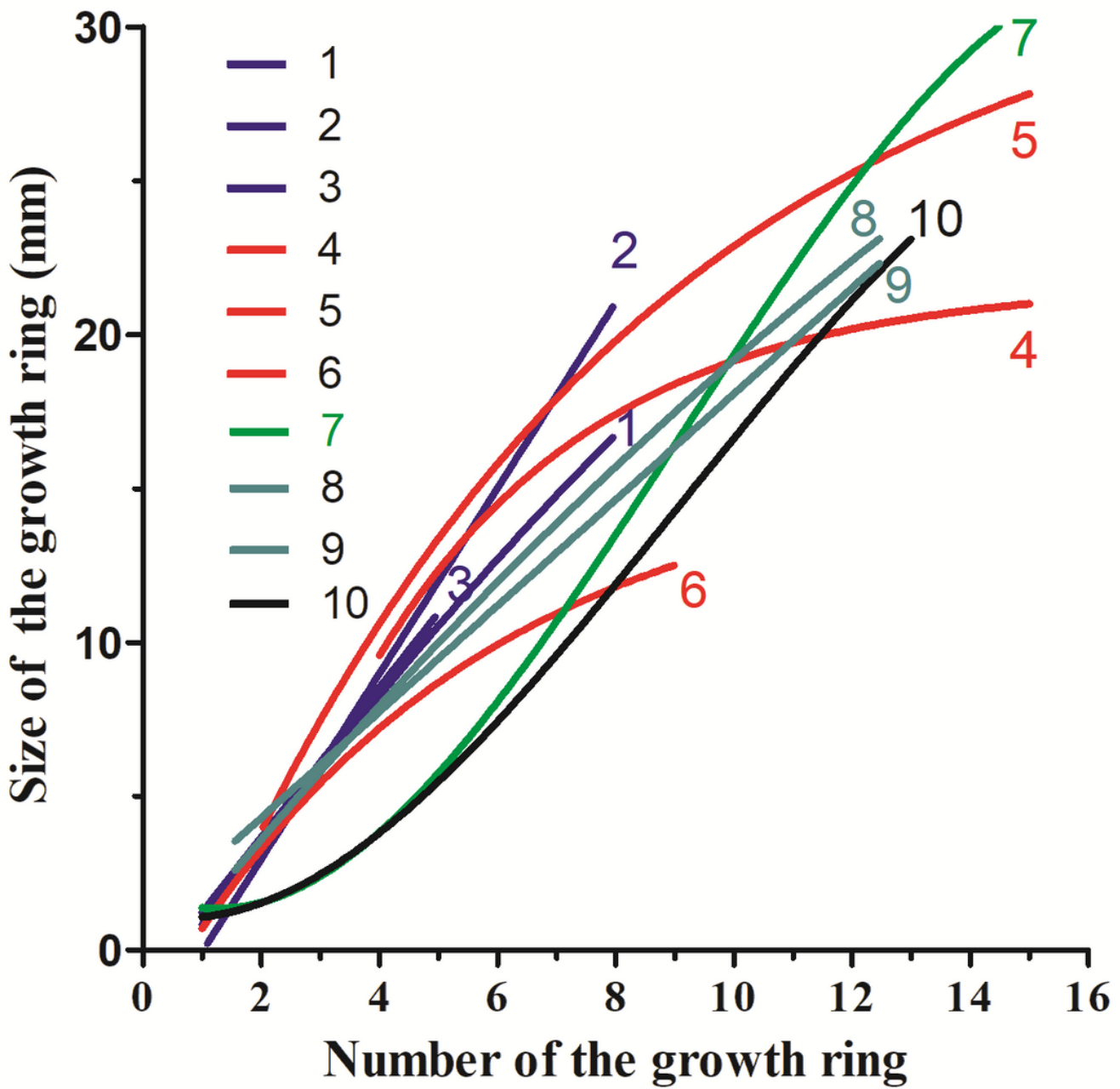


Figure 9

Reconstruction of the linear growth of *Macoma calcarea* in different parts of the range. 1-3 – White Sea (Lisitsyna et al. 2017): 1- depth 10-15 m, 2 - depth 10-18 m, 3 - depth 35-40 m; 4-6 – Western Greenland (Petersen 1978): 4- depth 3-13 m, 5 - depth 3-13 m, 6 - depth 3-107 m; 7 - Pechora Sea (depths 8-52 m) (Gerasimova et al. 2019); 8-9 - Eastern Barents Sea, off the Novaya Zemlya Archipelago (Noskovich 2021): 8 – depth shallower than 100 m; 9 - depth greater than 100 m; 10 - Kara Sea (depth 21-53 m) (our data)

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