



**Abundance and spatial distribution of two infaunal bivalves
— *Macoma balthica* and *Cerastoderma edule* on the Barents
Sea intertidal**

Journal:	<i>Journal of the Marine Biological Association of the United Kingdom</i>
Manuscript ID:	Draft
Manuscript Type:	Special Issue - EMBS European Marine Biology Symposium
Date Submitted by the Author:	n/a
Complete List of Authors:	Nazarova, Sophia; St-Petersburg State University, Ichthyology and Hydrobiology ; Russian State Pedagogical University, Zoology Shunkina, Ksenia; Zoological Institute RAS, Laboratory of Evolutional Morphology Genelt-Yanovskiy, Evgeny; Saint-Petersburg State University, Ichthyology and hydrobiology; Baltic Fund for Nature,
Keywords:	<i>Cerastoderma edule</i>, cockle, <i>Macoma balthica</i>, Barents sea, spatial distribution, abundance, microdistribution, species ranges
Abstract:	<p>Density distribution of the common infaunal bivalves, <i>Macoma balthica</i> and <i>Cerastoderma edule</i>, was studied along the Murman coast of the Barents Sea during 2002–2010. Our sampling program included two scales of abundance variability – geographic heterogeneity of mean bivalve density at different sites and patterns of spatial arrangement of individuals within the tidal beds. In both species abundance was mostly higher in West Murman in contrast to East Murman. Highest density of <i>Macoma balthica</i> reaching 1535 ind. m⁻² was observed in the Kola Bay. <i>Cerastoderma edule</i> was less abundant, its density rarely exceeded 10 ind. m⁻² in all but one site, where 282 ind. m⁻² was registered. Patterns of spatial arrangement of individuals were site-specific in both species, and all three distribution types (uniform, random and aggregated) were detected. Reconstruction of abundance distribution across species geographic ranges revealed that both range shapes does not match "abundant-centre" pattern, having features of ramped north in <i>Macoma balthica</i> and ramped south in <i>Cerastoderma edule</i>.</p> <p>Nazarova_et_al_abstract.doc</p>

SCHOLARONE™
Manuscripts

For Review Only

Abundance and spatial distribution of two infaunal bivalves — *Macoma balthica* and *Cerastoderma edule* on the Barents Sea intertidal

Sophia Nazarova^{1,2,*}, Evgeny Genelt-Yanovsky¹, Ksenia Shunkina³

¹ – Department of hydrobiology and ichthyology, St-Petersburg State University, 16 linia V.O., 29, St-Petersburg, 199178, Russia

² – Department of zoology, Russian State Pedagogical University, Moyka emb., 48, St-Petersburg, 191186, Russia

³ – Laboratory of Evolutional Morphology, Zoological Institute RAS, Universitetskaya emb., 1, St-Petersburg, 199034, Russia

* Corresponding author: Sophia Nazarova, e-mail: sophia.nazarova@gmail.com

*Density distribution of the common infaunal bivalves, *Macoma balthica* and *Cerastoderma edule*, was studied along the Murman coast of the Barents Sea during 2002–2010. Our sampling program included two scales of abundance variability – geographic heterogeneity of mean bivalve density at different sites and patterns of spatial arrangement of individuals within the tidal beds. In both species abundance was mostly higher in West Murman in contrast to East Murman. Highest density of *Macoma balthica* reaching 1535 ind. m⁻² was observed in the Kola Bay. *Cerastoderma edule* was less abundant, its density rarely exceeded 10 ind. m⁻² in all but one site, where 282 ind. m⁻² was registered. Patterns of spatial arrangement of individuals were site-specific in both species, and all three distribution types (uniform, random and aggregated) were detected. Reconstruction of abundance distribution across species geographic ranges revealed that both range shapes does not match “abundant-centre” pattern, having features of ramped north in *Macoma balthica* and ramped south in *Cerastoderma edule*.*

Keywords: *Cerastoderma edule*; cockle; *Macoma balthica*, Barents sea, spatial distribution, abundance, microdistribution, species ranges

25 INTRODUCTION

26 Patterns of species' abundance at the biogeographic extremes, such as Arctic for boreal species, may
27 provide insights into such essential issues in ecology as identification of borders between adjacent
28 biogeographic regions and causes of species range limits. Large-scale distribution of species
29 abundance is also a key element of applied sciences such as planning of protected areas and
30 designation of species into regional Red Lists. A widespread paradigm, known as «abundant-centre
31 hypothesis» (ACH) is widely used to test whether the highest species abundance belongs to the
32 range centre and declines towards range edges (Sagarin et al., 2006). It is based on Brown's
33 principle (Brown, 1984) and Hutchinson's niche concept (Leibold, 1995) assuming positive
34 connection between local abundance and living conditions.

35 Intertidal fauna is an ideal test system for studying latitudinal gradients. Many intertidal and
36 high subtidal marine invertebrates have extended ranges with distinct north (or northeastern) and
37 south (or southwestern) limits characterized by diametrically opposed combination of
38 environmental conditions. Recent studies on wide-spread marine coastal invertebrates have shown
39 that abundance centre pattern does not apply to all species equally, and even closely related species
40 could show different spatial patterns (Sagarin, Gaines, 2002; Rivadeneira et al., 2010).

41 Empirical approaches to quantify abundance in different parts of the range vary widely. One
42 of the main challenges for examining the abundant centre pattern is a logistical difficulty of
43 sampling throughout the whole species range. Particularly, it could be a problem to get adequate
44 samples from the range edge, where local populations are not stable in time and can spontaneously
45 become extinct and later reoccupy suitable habitats (Sagarin, Gaines, 2002; Sexton et al., 2009).

46 Species ranges are not stable in time, often shifting, expanding and contracting (Gaston,
47 2003). Fluctuations of environmental variables, such as climate oscillations, may alter population
48 fitness at the distribution limits and range shifts can lag behind environmental changes (Pfenninger
49 et al., 2007; Svenning et al., 2008). Marginal populations exhibit greater temporal variability in

abundance being near the species' limit of environmental tolerance, especially in extreme years (Gaston, 2009). Since temporal variation can introduce errors in estimation of spatial abundance distribution,, it is highly important to apply monitoring data series to improve the understanding of differences in abundance between central and edge populations (Holt, Keitt, 2000; Johnstone, Chapin, 2003). The spatial distribution and patchy structure of population density are also likely to determine range limits. Edge populations usually are smaller and more spatially fragmented than populations in the centre of the range (Brown et al., 1995). They may exhibit reductions in diversity and in number of immigrants due to spatial arrangement only, thus resulting in an isolation-by-distance effect (Sexton et al., 2009).

Here, we present the results of the study of abundance distribution, spatial arrangement of individuals and dynamics of two intertidal bivalves *Macoma balthica* and *Cerastoderma edule* from the Barents Sea, where they are expected to show controversial life history traits due to differences in populations position within the species' ranges. *Macoma balthica* is no longer regarded as one single species, but as a complex of Pacific *Macoma balthica balthica* and Atlantic *Macoma balthica rubra* subspecies (Nikula et al., 2007). In Europe this complex spreads from Bay of Biscay up north to the western Kara sea. Pure *M.balthica balthica* north distribution limit belongs to the Varanger Peninsula, while populations in the White and Barents seas are proved to form a broad «hybrid swarm» - their genetic composition is intermediate between Atlantic and Pacific forms (Strelkov et al., 2007).

Distribution range of *Cerastoderma edule* is limited by the Barents sea in the north and by Morocco Atlantic coast in the south. Cockle beds reach highest densities and biomass in the North and Irish Seas, where commercial fisheries of cockles persisted for centuries (Dare et al., 2004; Beukema, Dekker, 2009; Woolmer, 2010). Earlier, we proposed that *C.edule* generally follow the ACH pattern across the range with a significant decline in abundance near the North-Eastern range edge, but in case of successful recruitment, distinct local cockle populations in the Barents sea

could show much higher densities (Genelt-Yanovskiy et al., 2010). We hypothesize (1) that *Cerastoderma edule*, as a temperate-zone species, will demonstrate lower densities of individuals at the range edge and scattered distribution of local populations across the Murman shore of the Barents sea as in comparison to *Macoma balthica*, and (2) non-random density distribution of individuals within the local populations on most of tidal flats for both species.

MATERIALS AND METHODS

Study area

Murman coast is a northern border of the Kola Peninsula with a coastal line length of about 700 km, including numerous bays and fiords. The longest, Kola Bay, divide Murman coast into two regions: Western Murman and Eastern Murman. These two parts demonstrate different environmental conditions, as the effects of Gulf Stream drop sharply from west to east. After E.F. Gourjanova, I.G. Zaks and P.V. Ushakov (Gourjanova & Ushakov, 1929; Gourjanova et al., 1929; Gourjanova et al., 1930) we consider Western Murman, Kola inlet and Eastern Murman as three distinct regions. Owing to gradient changes in environment this whole area has transitional biogeographical status - from boreal to arctic zone (Zenkevich, 1963).

Sampling

We used two different quantitative sampling procedures to resolve all the given problems: (i) random sampling for evaluation of mean abundance across Murman coast and (ii) regular grid small-scale sampling aimed to analyze the spatial arrangement of bivalve density (microdistribution) within the tidal flats. All samples were sieved through 1 mm mesh.

I. Random sampling was conducted at 18 sites (all for *C. edule* and 12 of them for *M. balthica*) (table. 1). The sampling took place in July–August, from 2002 to 2010. We took five samples at each tidal level in all soft-bottom sites studied. We used 5 cm deep cores, with a surface

98 area of $1/30 \text{ m}^{-2}$ at the sites inhabited by *Macoma* alone, and with area of $1/10 \text{ m}^{-2}$ for sites where
99 *acoma* and *Cerastoderma* occurred together.

100 II. For short-term sampling for microdistribution we adopted (scaled down) regular grid
101 sampling procedure from Trush et al (1989). We allocated a single sample grid site in each of three
102 bays: Dalne-Zelenetskaya (2007), Yarnyshnaya (2008) and Pala (2008). In all three bays all the
103 samples were collected at middle intertidal zone (level), since it is known to be the most typical
104 habitat for the both species (Gourjanova & Ushakov, 1929; Gourjanova et al., 1929; Gourjanova et
105 al., 1930). Each sampling site ($12 \times 7.5 \text{ m}$) was divided into twelve equal sectors. From each sector
106 three sediment cores ($1/30 \text{ m}^{-2}$) were taken. The position of each core was assigned from randomly
107 derived cartesian coordinates. We took a total of 36 samples from each bay. In Dalne-Zelenetskaya
108 bay in 2008 we collected twice the number of cores from two adjacent sites. In all cases, we
109 extracted both species from all samples.

110 Using data from the sampling in the Dalne-Zelenetskaya bay taken in 2008, we also illustrated
111 microdistribution of *C. edule*. We recorded the location and collected every cockle individual found
112 across one of the two $12 \times 7.5 \text{ m}$ sampling sites. Finally, a total distribution map of the sapling site
113 with spatial resolution of 5 cm was created. All collected bivalves were sorted, identified and
114 counted. We have measured the shell length and individual weight of every cockle in samples.
115 Additionally, the mollusc age was determined by counting shell annual growth marks.

116 **Statistical analysis**

117 Identical statistical procedures for both species were employed. From the data obtained with the
118 first sampling procedure, we estimated the larger-scale patterns of abundance across the Murman
119 coast. We started with describing the abundances from each site. We used both medians and means
120 as measures of central tendency and created Tukey boxplots (Tukey, 1976) to illustrate abundance
121 variability. Data on abundance from individual samples from one site was used for plotting.
122 Kruskal-Wallis test (Hollander, Wolfe, 1973) was used for comparison between regions.

Spatial patterns were investigated with correlograms based on Moran's spatial autocorrelation coefficient, $I(g)$ (Sokal, 1979, Bjornstad, 2013). Samples within sites were grouped according to distances, estimated directly from the differences in cartesian coordinates. To calculate Moran's $I(g)$ we sorted samples into distance classes of 1 m. The null hypotheses of $I(g)=0$ were checked with permutation test. Thus we clarified the nature of patterns and estimated patch sizes.

We tested both vertical and horizontal spatial gradients of abundance across the shore using Kendall's rank correlations (Hollander, Wolfe, 1973).

All calculations were done with R (R-core, 2014). In all cases, statistical significances were tested at 5% probability level.

RESULTS

Bivalve abundance at the Murman coast of the Barents Sea

The abundance of *M. balthica* at the sites taken at the West Murman and Kola Bay varied from hundreds to thousands individuals per square meter. Maximum abundance (more than 3000 ind. m⁻²) was observed in Kola Bay at Cape Abram site. At the East Murman *M. balthica* abundance was significantly lower (less than 100 ind. m⁻² at the most sites). The lowest abundance (about 30 ind. m⁻²) was observed in Dalne-Zelenetskaya bay (East Murman) (figure 1, A). It was also shown that *M. balthica* mean abundances were significantly different at three regions of the Murman coast (Kruskal-Wallis test: $\chi^2 = 17.6$, $p < 0.0001$).

Alive individuals of *C. edule* were revealed only at 11 sites out of 18. We haven't found any alive individuals at bays Klimkovka, Dolgaya, Tyuva, Gavrilovo, Drozdovka, Ivanovskaya and Gremikha. The highest abundance of cockles were found at Ura-bay, West Murman (282±68 ind./m⁻²) (figure 1, B). The other site with rather high abundance was found also in the Western Murman region – it was Pala-bay, West Murman (45±9 ind. m⁻²). In 2007 cockle abundance at this site decreased to 10 ind. m⁻². Cockle abundance was notably lower at all other sites (less than 10

ind. m⁻² at most sites) (figure 1, B). Mean abundance at the West Murman was significantly higher than at other two regions. (Kruskal-Wallis test: $\chi^2 = 21.4$, $p < 0.001$).

At sites Pechenga, Ura, Retinskoe, Bolshaya Volokovaya we have found only a few empty shells in cores, but searching out of sampling areas some alive individuals were found. At some sites (Gavrilovo, Drozdovka) we have found only empty shells of *C. edule*. Shelpino population completely become extinct after 2009.

Microdistribution

No spatial patterns were found for *M. balthica* in Dalne-Zelenetskaya bay in 2007. Thus, we supposed that probably the sample site size could be too small, so it was 2 times enlarged in 2008. After that we found that significantly positive Moran's I was for lag 1.5–2 m and significantly negative for lag 4 m (figure 2, B). It allows to suppose that there could be small *Macoma* patches (diameter was equal to the core diameter, 1/30 m⁻²) that aggregate to a larger one.

No spatial patterns for *Macoma* were found in Yarnushnaya bay in 2008. At Pala bay patches with diameter about 2–4 m were found (figure 2, A). Series of negative significant Moran's I may indicate a gradient distribution at this site. According to the Kendall test we conclude that there was abundance gradient towards a freshwater stream crossing the intertidal zone ($\tau = 0.55$; $p < 0.0001$).

As *Macoma* abundance in Pala bay was rather high, we were able to investigate spatial distribution of molluscs of different age groups (table 2). A horizontal gradient was revealed for clams aged 2+, 3+ and 5+. Elder *Macoma* were aggregated in big patches with diameter about several meters. The abundance of the oldest individuals was low, their distribution pattern was evaluated as random.

For *C. edule* we found aggregation patches only in Yarnyshnaya and Pala bays. Patch diameter was about 3 meters in Yarnyshnaya bay (figure 3, B), and in Pala bay at investigation polygon there was only one huge aggregation with diameter about 5 meters (figure 3, A). At Dalne-Zelenetskaya bay in 2008 we've arranged individual mapping of *C. edule* within the similar 12 x 7,5

172 polygon (figure 4). Totally 86 cockles were found at 90 square meters, which was equal to mean
173 abundance of 0.96 ind. m⁻².

174 DISCUSSION

175 Our results generally match with the expectation that amphi-boreal species *Macoma balthica* will
176 show higher densities in the Barents Sea in comparison to the more temperate-zone *Cerastoderma*
177 *edule*. Cockle is supposed to be the most sensitive to low air temperatures bivalve on European
178 shores - severe winters were shown to cause mass mortalities among adult *Cerastoderma edule* in
179 the Wadden sea (Strasser et al., 2001). Which exactly effects of severe winters are more critical for
180 cockle survival is still unclear, but probably the sudden rise of the air temperature in subsequent
181 spring may be even more crucial than winter freezing of upper bottom level during low tides
182 (Strasser et al., 2001).

183 Conversely, long-term monitoring data from the Wadden sea provided evidences that high
184 winter temperatures negatively affects *Macoma* population dynamics in numerous ways and that
185 southern distribution range limit of *Macoma* has shifted several hundreds of kilometers north during
186 last decades (Beukema et al., 2009). Community-level analyses revealed that mild warm winters in
187 the Wadden sea give advantage to recruitment in decapods *Crangon crangon* and *Carcinus maenas*,
188 which in turn essentially feed on postlarvae of bivalves *Macoma balthica*, *Cerastoderma edule*,
189 *Mya arenaria* and *Mytilus edulis* (Beukema, Dekker, 2014). Barents Sea is lacking *Carcinus*
190 *maenas*, its north distribution edge belongs to North Norway. *Crangon crangon* also cannot be
191 regarded as important predator on the Barents Sea intertidal because it does not seem to form
192 permanent populations in the Murman coast (Kuznetsov, 1960).

193 Populations of *Macoma balthica* in the SW Barents Sea (Murman coast) are certainly not
194 marginal within the species' European part of the range – *Macoma* also occur in the Kara sea on the
195 North-East and quite typical for the White Sea intertidal communities, where it reaches high
196 densities (Semenova, 1974; Denisenko et al., 2003; Strelkov et al., 2007; Gerasimova, Maximovich,

2013). According to our data, mean *Macoma* abundance was significantly lower in East Murman sites in comparison to West Murman and Kola Bay sites. At West Murman and in Kola Bay clam densities are comparable with their densities in the White Sea, in the Baltic Sea and in the nearest waters – the northern part of the Norwegian Sea (for example Semenova, 1974; Aschan, 1988; Bostrom, Bonsdorf, 2000; Oug, 2001; Varfolomeeva, Naumov, 2013; Rousi et al., 2013; Gerasimova & Maximovich, 2013). At the East Murman *Macoma* abundance is lower than in the other regions. We found similar abundances in the south part of the Norwegian sea and in the Wadden Sea (Sneli, 1968; Beukema, 1976; Jensen, Jensen, 1985; Reise et al., 1994).

This difference could be interpreted by difference in general environmental conditions between West and East Murman. West Murman is an area of numerous fjord-like bays, among which Kola Bay is the longest (57 km) and Pechenga and Ura are more typical – 16 and 19 km long respectively. East Murman coast contrary is comparatively straight. Also, western current, a branch of Gulf Stream, dominates the nearshore hydrodynamics in East Murman, while longer bays of West Murman are more isolated and thus provide more stable conditions (Denisov & Dzhenyuk, 1995).

Regional heterogeneity was declared even within West Murman and Kola Bay (figure 1A). Among all sites, the highest density was recorded in the inner part of the Kola Bay – in Cape Abram site (figure 1). Nagornoe, nearest to Cape Abram site, situated on the opposite shore of Kola bay, demonstrated lower clam density. We suppose that lower abundances in Nagornoe could be a consequence of its location nearby to the sewer outlet of city of Murmansk. It is well known, that *Macoma* uses two types of feeding modes – suspension-feeding, more typical for clams living on sandy bottoms, and deposit-feeding which is usual for *Macoma* from muddy habitats (Olafsson, 1989). Despite we didn't conducted organic content and grain-size analysis for Cape Abram and Nagornoe sites, it is obvious that the tidal zone around sewer outlets (Nagornoe) contains additional amounts of silt as compared to background values (Littler & Murray, 1975; de-la-Ossa-Carretero et

al., 2012). Thus, in muddy habitats, such as Nagornoe, *Macoma* shows density-related effects due to intraspecific competition for food and space, at least on growth levels (Olafsson, 1989).

Densities of *M.balthica* in Ivanovskaya, the easternmost site for this species in our dataset, were dissimilar with other East Murman localities, because in this site *Macoma* appeared to be more subtidal than intertidal species – it occurs just below the LWL. Subtidal *Macoma balthica* population was previously reported in the Pechora sea (SE part of the Barents sea) with mean densities of 654 ind./m², which is twice lower than in Ivanovskaya (Denisenko et al., 2003).

Our data suggest that *Macoma balthica* abundance distribution within the species range does not clearly follow the “abundant centre” (figure 5, A) and is more likely a “ramped north” (for names of distribution shapes see Sagarin & Gaines, 2002). Surprisingly, mean adult (>1 mm) *Macoma* densities in West Murman local populations were more similar to the White and Baltic Seas, and were higher than long-term mean values available for North Sea and Bay of Biscay (see appendix A). This result corresponds with the distribution of Atlantic *Macoma balthica rubra* and Pacific *Macoma balthica balthica* lineages in Europe (Nikula et al., 2007; Strelkov et al., 2007). European Atlantic *M.b.rubra* inhabits North Sea and Northeast Atlantic coasts, while *M.b.balthica* occurs together *M.b.rubra* in the Baltic and northern marginal seas and is regarded as a result of trans-Arctic invasion in early Holocene (Nikula et al., 2007).

Mean densities of adult *Cerastoderma edule* on the Murman coast of the Barents Sea, varying in most sites around 10 ind. m⁻² were generally lower than in other parts of the species range (Beukema, 1989; Ivell, 1989; André, Rosenberg, 1991; Bachelet et al., 1992; Ramon, 2003; Dare et al., 2004). Very similar to the Barents Sea cockle density was previously reported from Tromsø, North Norway (Oug, 2001). That data also supports hypothesis that low abundance is typical feature of the northern part of the species range. *Cerastoderma edule* abundance distribution pattern within the range could be named as “abundant centre” (figure 5, B). Taking into account that at

southernmost distribution limit, Merja Zerga (Morocco), cockle density may reach 1200 ind m⁻² with long-term mean of 638 ind m⁻², abundance pattern could be probably transitional between typical “abundant centre” and “rumped south”, because (Gam et al., 2010).

Current easternmost *Cerastoderma* local population is located in Trashina bay (~68° 59' N, ~36° 30' E), we didn't find any alive cockles further east. However, in Drozdovka bay (~100 km east from Trashina) we've found out two non-fossilized cockle shells, which means that temporary outbreak settlement of this species occurred here some years ago. Murman coast clearly is a dynamic range edge for *Cerastoderma*, and thus in five other sites (Pechenga, Retinskoe, Tuva, Bolshaya Volokovaya, Gavrilovo) there was no possibility to estimate cockle density using standard sampling methods and only shells were found. No cockles were also found in the inner part of the Kola Bay, Cape Abram and Nagornoe (figure 1,B). We suppose that it could be explained by known sensitivity of *Cerastoderma* to pollution load (Savari et al., 1989), which should be significant near the city and port of Murmansk, largest coastal industrial area in the Barents Sea region.

Cerastoderma edule population dynamics has a very typical feature of periodically occurring mass mortality events, when adult densities sharply reduces from thousands of individuals to single cockles per square meter due to a variety of factors. After that slow population recovery takes place (Strasser et al., 2001; Malham et al., 2012; Callaway et al., 2013). In the Wadden sea during periods, called after Ducrotoy et al. (1991) as “recovery”, cockle density may reach 54000 ind. m⁻² including individuals of all age groups (Malham et al., 2012). According to our study, *Cerastoderma* local population in Ura bay on West Murman unambiguously had features of recovery phase of population dynamics in 2010 after “crisis” phase observed in 2005 (figure 1, B). During our first visit, only solitary individuals were found across the tidal flat, while in 2010 mean cockle density was 282 ind m⁻², which is highest density value for the Barents sea. Our results on cockle local population recovery in Ura bay support the dependence of Barents sea populations of invertebrates and pelagic fish on larval drift from west (Gjøsaeter, 1995; Mikkelsen & Pedersen,

2004; Strelkov et al., 2007).

Spatial aggregation may form on different scales. It could be observed at geographic distribution level, where distribution of populations and their abundance is a response of availability of suitable habitats, or simply could be driven by patchy structure of the biotope, which is critically important for distribution of individuals (Thrush et al., 1989; Kraan et al., 2010; Santos et al., 2012). Remarkably low *Cerastoderma* and *Macoma* densities in East Murman local populations provoked a further study of abundance distribution of these species within the tidal flats. Since the beginning it was obvious that cockles have non-random distribution during low tides, as the sampling of qualitative material for our previous study on dynamics and growth of *Cerastoderma edule* (Genelt-Yanovskiy et al., 2010) usually became easy right after the first mollusk was discovered, even in bays where quantitative estimation of density was not possible.

Our data show that spatial distribution patterns of *Cerastoderma* and *Macoma* were site-specific. Most significant non-random distribution of *Macoma* was observed in Pala bay, where density of smaller individuals gradually increased towards the streambed flowing through the central part of tidal flat, bigger clams formed broad patch and oldest individuals were arranged randomly (figure 2,A, table 2). Gradient pattern in younger *Macoma* is probably determined by higher availability of dissolved organic matter brought by the stream and thus lower competition with uniformly distributed adults.

Cerastoderma distribution on the Pala bay intertidal as well as in Yarnishnaya bay was also non-random, but cockle formed patchy aggregations 3–5 meters in diameter (figure 3,B). Experimental data suggested that the high abundance causes more uniform distribution of *Cerastoderma* individuals, but when density is low, cockles become more randomly distributed (Richardson et al., 1993). *Cerastoderma* is highly mobile species; each individual can crawl over 0.5 m during each tidal cycle, and thus distribution pattern changes over time (Richardson et al., 1993). In the Wadden sea, where *Macoma* and *Cerastoderma* may form patches with the size over

200 and 1000 meters respectively (Santos et al., 2012). In Dalne-Zelenetskaya bay cockles showed random distribution pattern at the chosen scale. Further attempt of individual location of cockles within the polygon revealed that even at low densities (figure 4), typical for the East Murman, cockles could be arranged uniformly within tens of meters.

Intertidal infaunal bivalves, inhabiting same area may demonstrate similar patterns of spatial distribution over tidal flats (Kraan et al., 2010; Santos et al., 2012). Within the present study we didn't evaluated abundance of the *Mya arenaria*, third infaunal bivalve species occur on the tidal flats of the Barents Sea, but more abundant in the White Sea (Gerasimova, Maksimovich, 2013). Sand gapers were observed in most sites where abundances of *Macoma balthica* and *Cerastoderma edule* were estimated, but only random distribution pattern was typical for *Mya*.

ACKNOWLEDGEMENTS

We are greatfull to all participants of Saint-Petersburg State university Barents Sea expeditions of 2002–2009 years for their help in the field work and to the administration of Kandalaksha State Natural Researve for supporting our activity.

FINANCIAL SUPPORT

The study was partially supported by RFBR grants No.12-04-01507-a, 12-04-10128-k, 13-04-10131-k, and SPbSU Action 2 research project No.1.38.253.2014.

REFERENCES

- André C. and Rosenberg R.** (1991) Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Marine ecology progress series*. Oldendorf 71(3), 227–234.
- Aschan M.** (1988) Soft bottom macrobenthos in a Baltic archipelago: Spatial variation and optimal sampling strategy. In *Annales Zoologici Fennici* 25 (2), 153–164.

- 320 **Bachelet G., Guillou J., and Labourg P. J.** (1992) Adult-larval and juvenile interactions in the
321 suspension-feeding bivalve, *Cerastoderma edule* (L.): field observations and experiments. In
322 *Marine eutrophication and population dynamics*. Olsen and Olsen, Fredensborg, pp.175–182.
- 323 **Beukema J. J.** (1976) Biomass and species richness of the macro-benthic animals living on the
324 tidal flats of the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 10(2), 236–261.
- 325 **Beukema J. J.** (1989) Long-term changes in macrozoobenthic abundance on the tidal flats of the
326 western part of the Dutch Wadden Sea. *Helgoländer Meeresuntersuchungen* 43(3–4), 405–
327 415.
- 328 **Beukema J. J., and Dekker R.** (2009) The intertidal zoning of cockles (*Cerastoderma edule*) in
329 the Wadden Sea, or why cockle fishery disturbed areas of relatively high biodiversity.
330 *Helgoland Marine Research* 63(4), 287–291.
- 331 **Beukema J. J., and Dekker R.** (2014) Variability in predator abundance links winter temperatures
332 and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Marine*
333 *Ecology Progress Series* 513, 1–15.
- 334 **Beukema J. J., Dekker R., and Jansen J. M.** (2009) Some like it cold: populations of the tellinid
335 bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Marine*
336 *Ecology Progress Series* 384, 135–145.
- 337 **Bjornstad O. N.** (2013) *ncf: spatial nonparametric covariance functions*. R package version 1.1–5.
338 <http://CRAN.R-project.org/package=ncf>
- 339 **Boström C. and Bonsdorff E.** (2000) Zoobenthic community establishment and habitat
340 complexity-the importance of seagrass shoot-density, morphology and physical disturbance
341 for faunal recruitment. *Marine Ecology Progress Series* 205, 123–138.
- 342 **Brown J. H., Mehlman D. W., and Stevens G. C.** (1995) Spatial variation in abundance. *Ecology*
343 76(7). 2028–2043.
- 344 **Callaway R., Burdon D., Deasey A., Mazik K. and Elliott M.** (2013) The riddle of the sands:
345 how population dynamics explains causes of high bivalve mortality. *Journal of Applied*

Ecology 50(4), 1050–1059.

Dare P.J., Bell M.C., Walker P. and Bannister R.C.A. (2004) *Historical and current status of cockle and mussel stocks in The Wash*. CEFAS Lowestoft. 85 pp.

Denisenko S. G., Denisenko N. V., Lehtonen K. K., Andersin A. B., and Laine A. O. (2003) Macrozoobenthos of the Pechora Sea (SE Barents Sea): community structure and spatial distribution in relation to environmental conditions. *Marine Ecology Progress Series* 258, 109–123.

Denisov V. V., Dzhenyuk S. L. (1995) Chapter 2. Abiotic conditions. Abiotic conditions of Kola Peninsula. In: *The Biological Resources of the Coastal zone of the Kola Peninsula. Modern State and Rational Usage*. Russian Academy of Sciences, Apatity, Murmansk, Russia. pp. 10–25. (In Russian)

Ducrotoy J. P., Rybarczyk H., Souprayen J., Bachelet G., Beukema J., Desprez M., ... and Ibanez F. (1991) A comparison of the population dynamics of the cockle (*Cerastoderma edule*, L.) in North-Western Europe. In: M. Elliott and J.-P. Ducrotoy. (eds.) *Estuaries and coasts: spatial and temporal intercomparisons. International Symposium Series, ECSA-19 Symposium*, Olsen and Olsen, Fredensborg. pp. 173–184

Gam M., de Montaudouin X., and Bazairi H. (2010) Population dynamics and secondary production of the cockle *Cerastoderma edule*: A comparison between Merja Zerga (Moroccan Atlantic Coast) and Arcachon Bay (French Atlantic Coast). *Journal of Sea Research*, 63(3), 191–201.

Gaston K. J. (2009) Geographic range limits of species. *Proceedings of the Royal Society B: Biological Sciences*, 276(1661), 1391–1393.

Genelt-Yanovskiy E., Poloskin A., Granovitch A., Nazarova S., and Strelkov P. (2010) Population structure and growth rates at biogeographic extremes: A case study of the common cockle, *Cerastoderma edule* (L.) in the Barents Sea. *Marine pollution bulletin*, 61(4), 247–

253.

Gerasimova A. V. and Maximovich N. V. (2013) Age–size structure of common bivalve mollusc populations in the White Sea: the causes of instability. *Hydrobiologia*, 706(1), 119–137.

Gjørøster H. (1995) Pelagic fish and the ecological impact of the modern fishing industry in the Barents Sea. *Arctic* 48(3), 267–278.

Gouryanova E.F., Zaks I.G. and Ushakov P.V. (1930) A littoral of western Murman. *Studies of the Seas of USSR* 2, 47–52 (In Russian)

Gouryanova E.F., Zaks I.G. and Ushakov P.V. (1929) A littoral of Kola bay. *Proceedings of the Leningrad Society of Naturalist* 60(2), 17–107. (In Russian)

Gouryanova E.F. and Ushakov P.V. (1929) A littoral of eastern Murman. *Studies of the Seas of USSR* 10, 5–40 (In Russian)

Hollander M. L. and Wolfe D.A. (1973) *Nonparametric Statistical Methods*. New York: John Wiley and Sons Perry Press.

Holt R. D. and Keitt T. H. (2000) Alternative causes for range limits: a metapopulation perspective. *Ecology Letters* 3(1), 41–47.

Ivell R. (1981) A quantitative study of a *Cerastoderma* – *Nephtys* community in the Limfjord, Denmark, with the special reference to production of *Cerastoderma edule*. *Journal of Molluscan Studies* 47, 147–170.

Jensen K. T. and Jensen J. N. (1985) The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 89(2), 157–174.

Johnstone J. F., and Chapin F. S. (2003). Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9(10), 1401–1409.

Kraan C., Aarts G., Van Der Meer J., and Piersma T. (2010) The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Ecology*

91(6), 1583–1590.

Kuznetsov V.V. (1960) *White Sea and biological features of its flora and fauna*. Moscow – Leningrad: Publishing House of the Academy of Sciences of the USSR. (In Russian)

Leibold M. A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology* 76(5), 1371–1382.

Littler M. M. and Murray S. N. (1975) Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology* 30(4), 277–291.

Malham S. K., Hutchinson T. H. and Longshaw M. (2012) A review of the biology of European cockles (*Cerastoderma* spp.). *Journal of the Marine Biological Association of the United Kingdom* 92(07), 1563–1577.

Mikkelsen N. and Pedersen T. (2004) How can the stock recruitment relationship of the Barents Sea capelin (*Mallotus villosus*) be improved by incorporating biotic and abiotic factors? *Polar Research* 23(1), 19–26.

Nikula R., Strelkov P. and Väinölä R. (2007) Diversity and trans-arctic invasion history of mitochondrial lineages in the north atlantic *Macoma balthica* complex (Bivalvia: Tellinidae). *Evolution* 61(4), 928–941.

Olafsson E. B. (1989) Contrasting influences of suspension-feeding and deposit-feeding populations of *Macoma balthica* on infaunal recruitment. *Marine Ecology Progress Series*, 55, 171–179.

de-la-Ossa-Carretero J. A., Del-Pilar-Ruso Y., Giménez-Casalduero F. and Sánchez-Lizaso J. L. (2012) Assessing reliable indicators to sewage pollution in coastal soft-bottom communities. *Environmental monitoring and assessment*, 184(4), 2133–2149.

Oug E. (2001) Polychaetes in intertidal rocky and sedimentary habitats in the region of Tromsø, northern Norway. *Sarsia* 86(1), 75–83.

Pfenninger M., Nowak C., and Magnin F. (2007) Intraspecific range dynamics and niche

evolution in *Candidula* land snail species. *Biological Journal of the Linnean Society* 90(2), 303–317.

Ramón M. (2003) Population dynamics and secondary production of the cockle *Cerastoderma edule* (L.) in a backbarrier tidal flat in the Wadden Sea. *Scientia Marina* 67(4), 429–443.

R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

Reise K., Herre E. and Sturm M. (1994) Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. *Helgoländer Meeresuntersuchungen* 48(2-3), 201–215.

Richardson C. A., Ibarrola I. and Ingham R. J. (1993) Emergence pattern and spatial distribution of the common cockle *Cerastoderma edule*. *Marine Ecology Progress Series* 99(1–2), 71–81.

Rivadeneira M. M., Hernáez P., Antonio Baeza J., Boltana S., Cifuentes M., Correa C., ... and Thiel M. (2010) Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life-history variation. *Journal of biogeography*, 37(3), 486–498.

Rousi H., Laine A. O., Peltonen H., Kangas P., Andersin A. B., Rissanen J., ... and Bonsdorff E. (2013) Long-term changes in coastal zoobenthos in the northern Baltic Sea: the role of abiotic environmental factors. *ICES Journal of Marine Science: Journal du Conseil* 70, 440–451.

Sagarin R. D., and Gaines S. D. (2002) The ‘abundant centre’ distribution: to what extent is it a biogeographical rule? *Ecology letters* 5(1), 137–147.

Sagarin, R. D. Gaines, S. D. and Gaylord B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* 21(9), 524–530.

- Santos S., Aarts G., Luttikhuizen P. C., Campos J., Piersma T., and van der Veer H. W.** (2012) Site-specific distribution of the bivalve *Scrobicularia plana* along the European coast. *Marine Ecology Progress Series* 471, 123–134.
- Savari A., Sylvestre C., Sheader M., Le Gal Y. and Lockwood A.P.M.** (1989) Stress studies on the common cockle (*Cerastoderma edule* L.) in Southampton Water. Topics in Marine biology. *Scientia Marina* 53(2-3), 729-735.
- Semenova N.L.** (1974) The distribution of the bivalve *Macoma balthica* (L.) in some inlets of Kandalaksha Bay of the White Sea. *Proceedings of the White Sea Biological Station of the Moscow State University* 4, 87–102. (In Russian)
- Sexton J. P., McIntyre P. J., Angert A. L. and Rice K. J.** (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40, 415–436
- Sneli J. A.** (1968) The intertidal distribution of polychaetes and molluscs on a muddy shore in Nord-Møre, Norway. *Sarsia* 31(1), 63–68.
- Sokal R. R.** (1979) Ecological parameters inferred from spatial correiograms. In: Patti, G. P., Rosenweig, M. (eds.) *Contemporary quantitative ecology and related econometrics*. Fairland, Maryland: International Co-operative Publishing House, pp. 167–196.
- Strasser M., Reinwald T. and Reise K.** (2001) Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria* in the Northern Wadden Sea. *Helgoland Marine Research* 55(3), 190–197.
- Strelkov P.P., Gancevich M.M. and Basova L.A.** (2001) Shell color polymorphism of *Macoma balthica* (Bivalvia, Tellinidae) in the White and Barents Sea. *Reports of Academy of Science* 376(1), 139–141. (In Russian)
- Strelkov P., Nikula R. and Väinölä R.** (2007) *Macoma balthica* in the White and Barents Seas: properties of a widespread marine hybrid swarm (Mollusca: Bivalvia). *Molecular ecology* 16(19), 4110–4127.

- 471 **Svenning J. C., Normand S. and Kageyama, M.** (2008) Glacial refugia of temperate trees in
472 Europe: insights from species distribution modelling. *Journal of Ecology* 96(6), 1117–1127.
- 473 **Tukey J. W.** (1976) *Exploratory data analysis*. Massachusetts: Addison-Wesley.
- 474 **Thrush S. F., Hewitt J. E. and Pridmore R. D.** (1989) Patterns in the spatial arrangements of
475 polychaetes and bivalves in intertidal sandflats. *Marine biology* 102(4), 529–535.
- 476 **Varfolomeeva M. and Naumov A.** (2013) Long-term temporal and spatial variation of
477 macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha
478 Bay, White Sea). *Hydrobiologia* 706(1), 175–189.
- 479 **Woolmer A. P.** (2010) Provisional Review and Advice of Cockle Management in the Burry Inlet.
480 *Shellfish Association of Great Britain, London*. 24 pp.
- 481 **Zenkevich L.A.** (1963) *Biology of the Seas of the U.S.S.R.* Moscow. Translated from Russian to
482 English by S. Botsharskaya. New York: Interscience Publishers.

Fig. 1. Mean abundance (N, ind.m⁻²) of *Macoma balthica* (A) and *Cerastoderma edule* (B) in the Barents sea. Samples are arranged from West to East. At the box-plots box marked Q1, median and Q3, whiskers marked 1.5 IQR. Mean abundance indicated at the top.

Fig. 2. *Macoma balthica*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Dalnezelenetskaya (B) bays. Autocorrelation coefficients represented by filled squares are significant (P< 0.05), open squares are non-significant

Fig. 3. *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by filled squares are significant (P< 0.05), open squares are non-significant

Fig. 4. Distribution of individuals of *Cerastoderma edule* within study polygon in Dalnezelenetskaya bay (2008).

Fig. 5. Abundance distribution of *Macoma balthica* (A) and *Cerastoderma edule* (B) within the species ranges. Circles squares are proportional to mean abundance. For sources of data see Appendix A.

Table 1. Investigation sites and sampling details

region	site	latitude, longitude	observation years
West Murman	Pechenga bay (PG)	69.58, 31.27	2005
	Ura bay (UR)	68.99, 36.51	2010
Kola bay	Pala bay (PL)	69.19, 33.37	2006-2007
	Retinskoe (RT)	69.11, 33.38	2005
	Cape Abram (AB)	68.98, 33.03	2008
	Nagornoe (NG)	68.90, 33.06	2005
	Tyuva	69.17, 33.63	2005
	Bolshaya Volokovaya	69.27, 33.62	2005
	Klimkovka	69.23, 34.64	2009
East Murman	Dolgaya	69.17, 33.63	2009
	Gavrilovo (GV)	69.17, 35.86	2008
	Yarnyshnaya (YA)	69.09, 36.05	2004 - 2008
	Dalnezelenetskaya (DZ)	69.11, 36.10	2002 - 2009
	Shelpino (SH)	69.10, 36.21	2005, 2008
	Porchnikha (PR)	69.08, 36.25	2006 - 2007
	Tryashina	68.99, 36.51	2008
	Drozdovka	68.30, 38.44	2008
	Ivanovskaya subtidal (IV)	68.29, 38.71	2008
	Gremikha	68.03, 39.85	2009

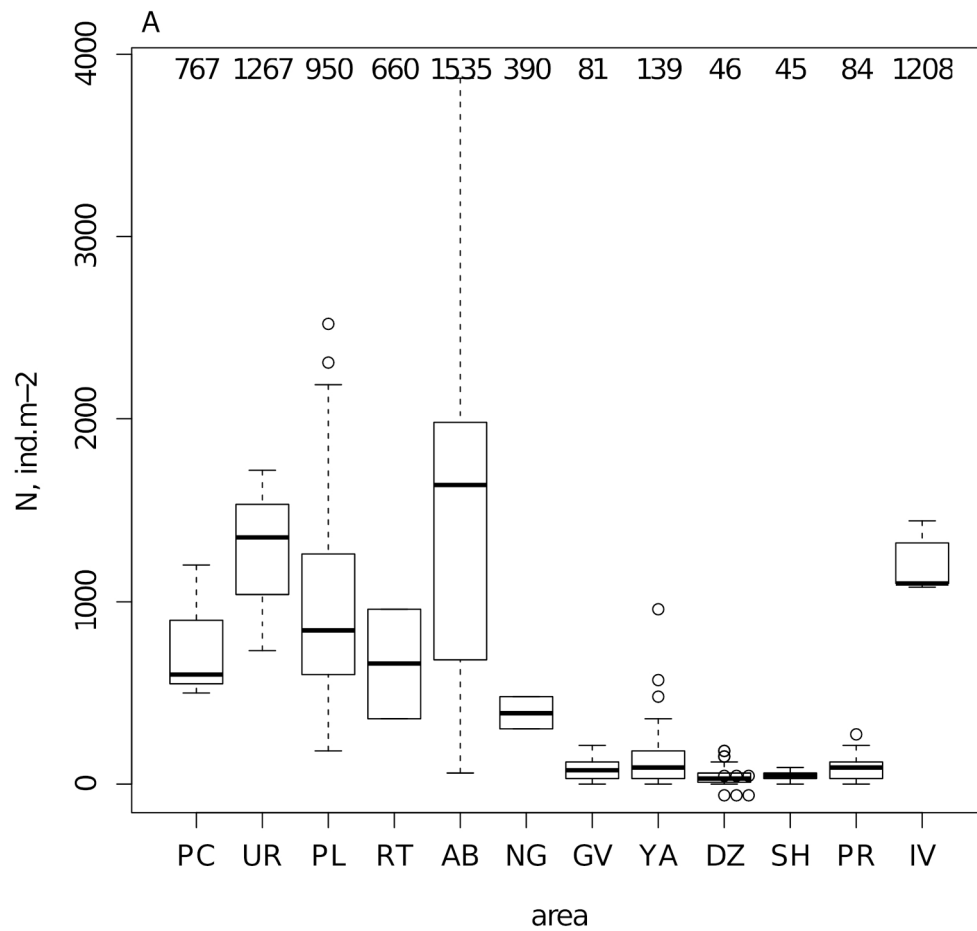


Fig. 1. Mean abundance (N, ind.m⁻²) of *Macoma balthica* (A) and *Cerastoderma edule* (B) in the Barents sea. Samples are arranged from West to East. At the box-plots box marked Q1, median and Q3, whiskers marked 1.5 IQR. Mean abundance indicated at the top.
171x161mm (300 x 300 DPI)

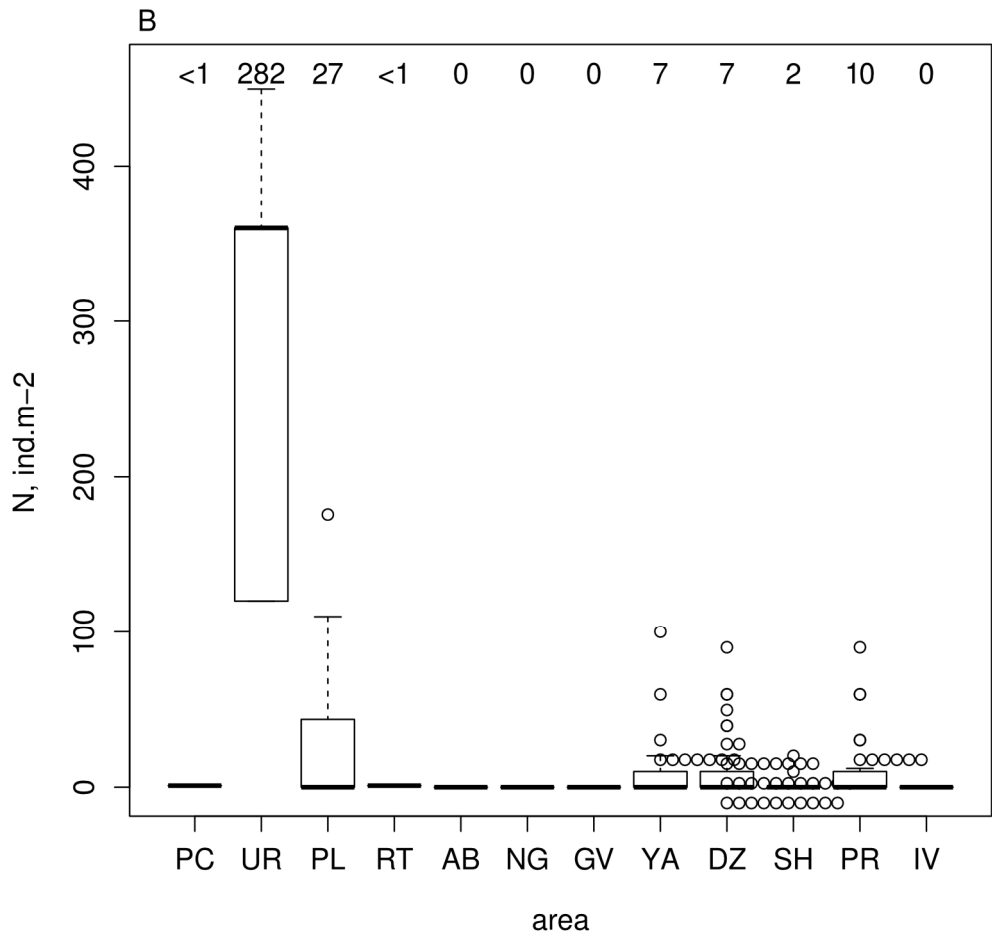


Fig. 1. Mean abundance (N, ind.m⁻²) of *Macoma balthica* (A) and *Cerastoderma edule* (B) in the Barents sea. Samples are arranged from West to East. At the box-plots box marked Q1, median and Q3, whiskers marked 1.5 IQR. Mean abundance indicated at the top.
170x161mm (300 x 300 DPI)

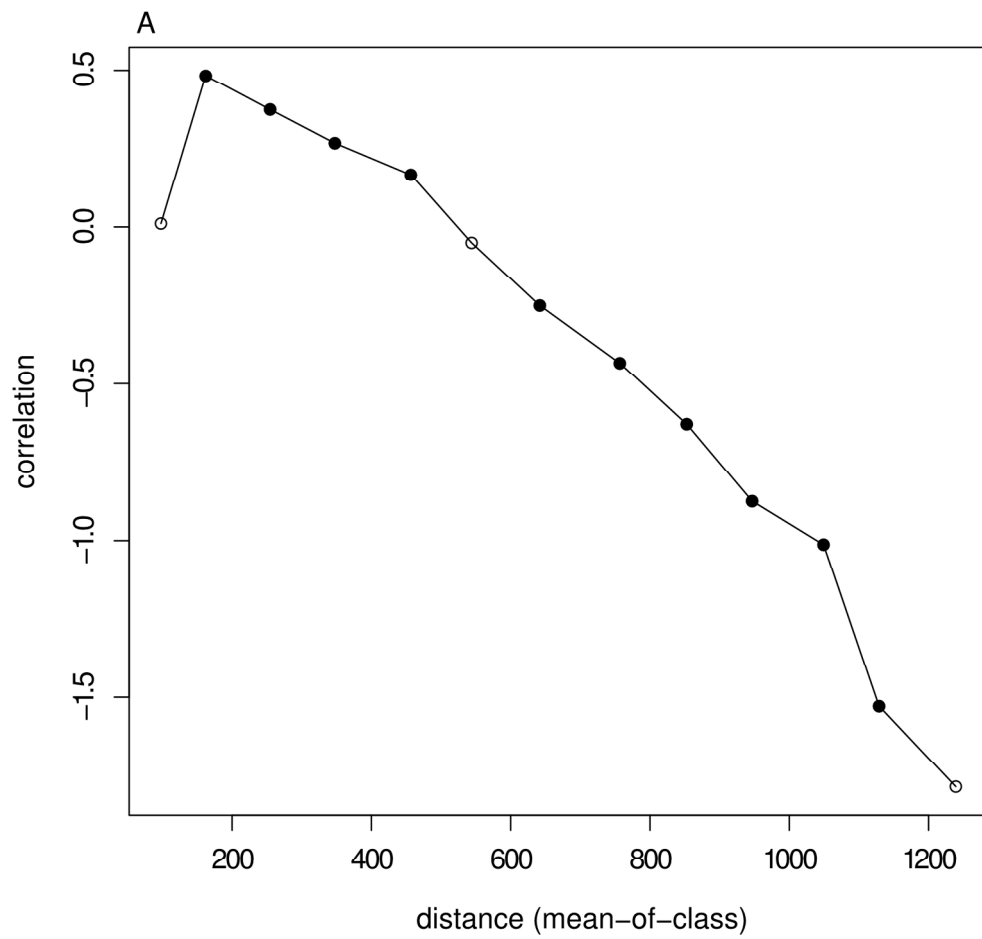


Fig. 2. *Macoma balthica*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Dalnezelenetskaya (B) bays. Autocorrelation coefficients represented by filled squares are significant ($P < 0.05$), open squares are non-significant
170x165mm (300 x 300 DPI)

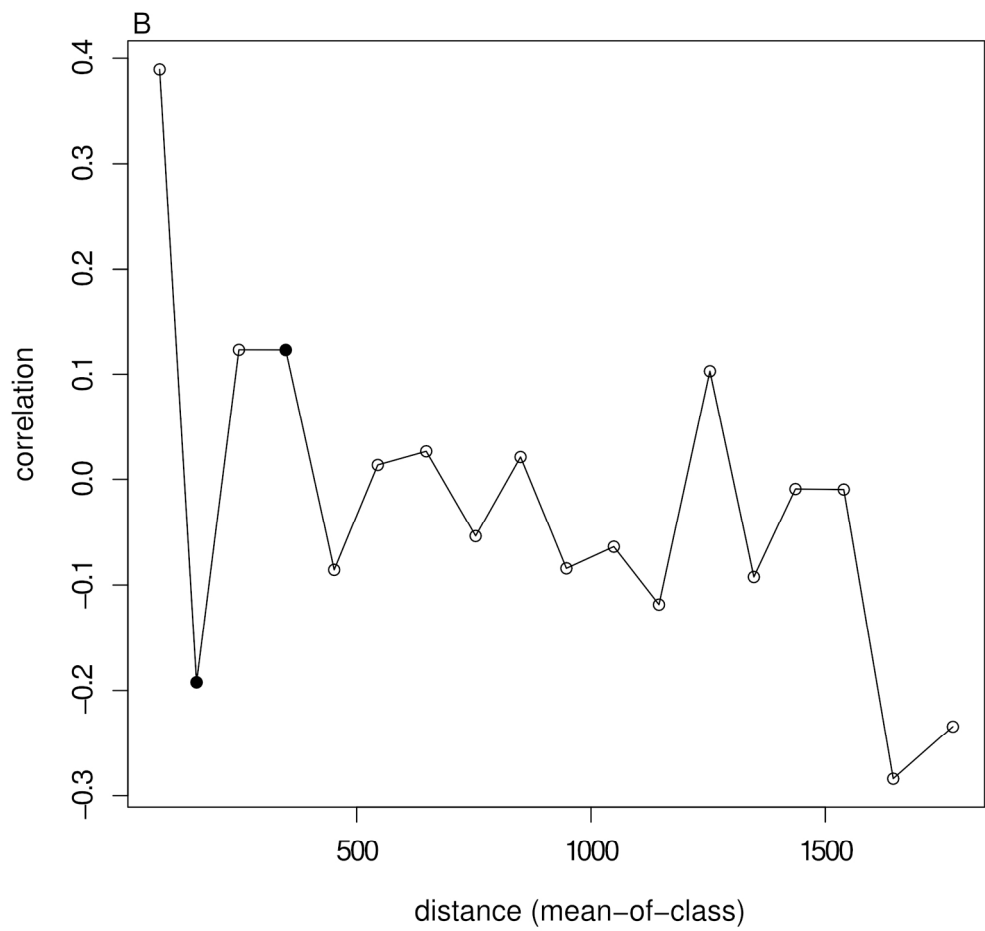


Fig. 2. *Macoma balthica*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Dalnezelenetskaya (B) bays. Autocorrelation coefficients represented by filled squares are significant ($P < 0.05$), open squares are non-significant

171x163mm (300 x 300 DPI)

Table 2. Spatial distribution of *Macoma balthica* of different ages in Pala bay (Kola bay, Barents sea). Results of analysis Moran's I spatial correlograms and gradient analysis with Kendall correlation.

age	spatial distribution	horizontal gradient		vertical gradient	
		Kendall τ	p-value	Kendall τ	p-value
1+	random	0.2	0.17	0.02	0.9
2+	gradient	0.45	0.0003 ***	0.2	0.07 *
3+	gradient	0.5	< 0.0001 ***	0.3	0.002 ***
4+	random	0.2	0.07 *	0.06	0.6
5+	gradient	0.43	0.0005 ***	-0.02	0.9
6+	random	0.2	0.03 **	-0.03	0.8
7+	single huge patch	0.02	0.9	-0.02	0.9
8+	single huge patch	0.3	0.01 ***	-0.2	0.04 **
9+	single huge patch	0.3	0.01 ***	-0.2	0.1
10+	patches diameter 1 and 3 meters	0.2	0.1	-0.2	0.08 *
11+	single huge patch	0.26	0.053 *	-0.1	0.3
12+	patches diameter 6 meters	0.1	0.3	-0.2	0.2
13+	random	0.1	0.4	0.04	0.7
14+	random	0.09	0.5	-0.15	0.3

Significance level: *** – 1%, ** – 5%, * – 10%.

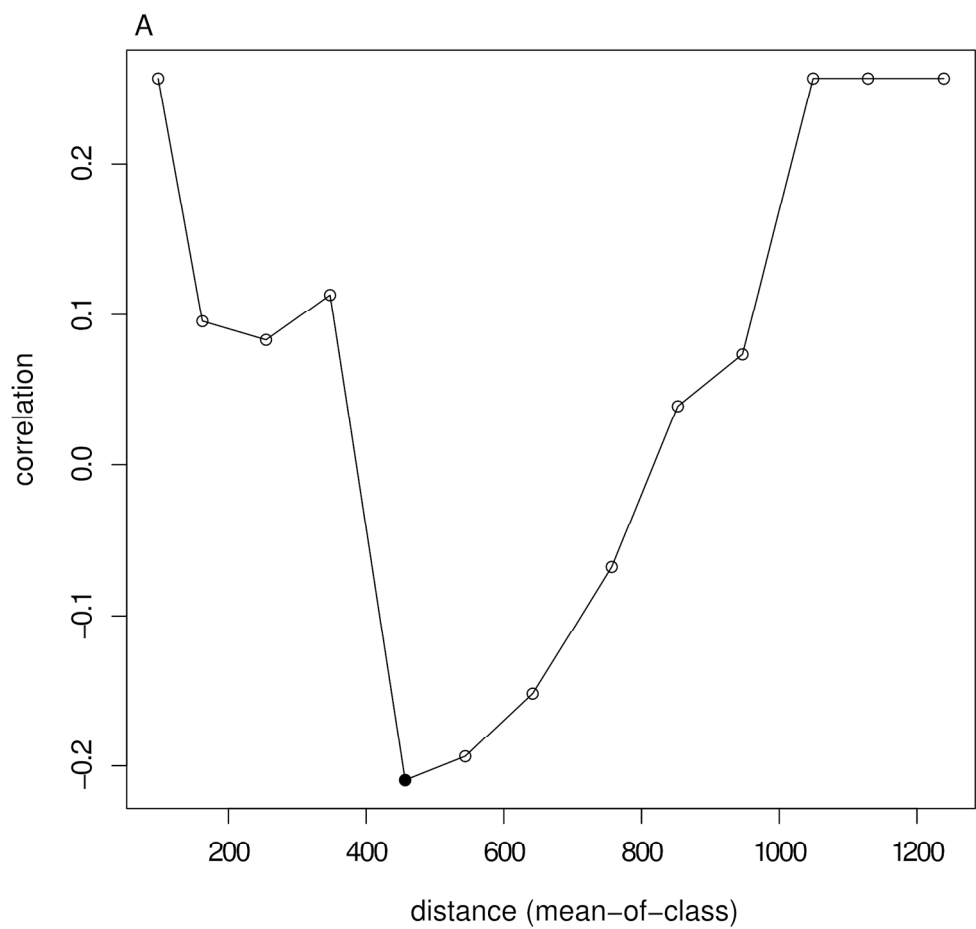


Fig. 3. *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by filled squares are significant ($P < 0.05$), open squares are non-significant

172x165mm (300 x 300 DPI)

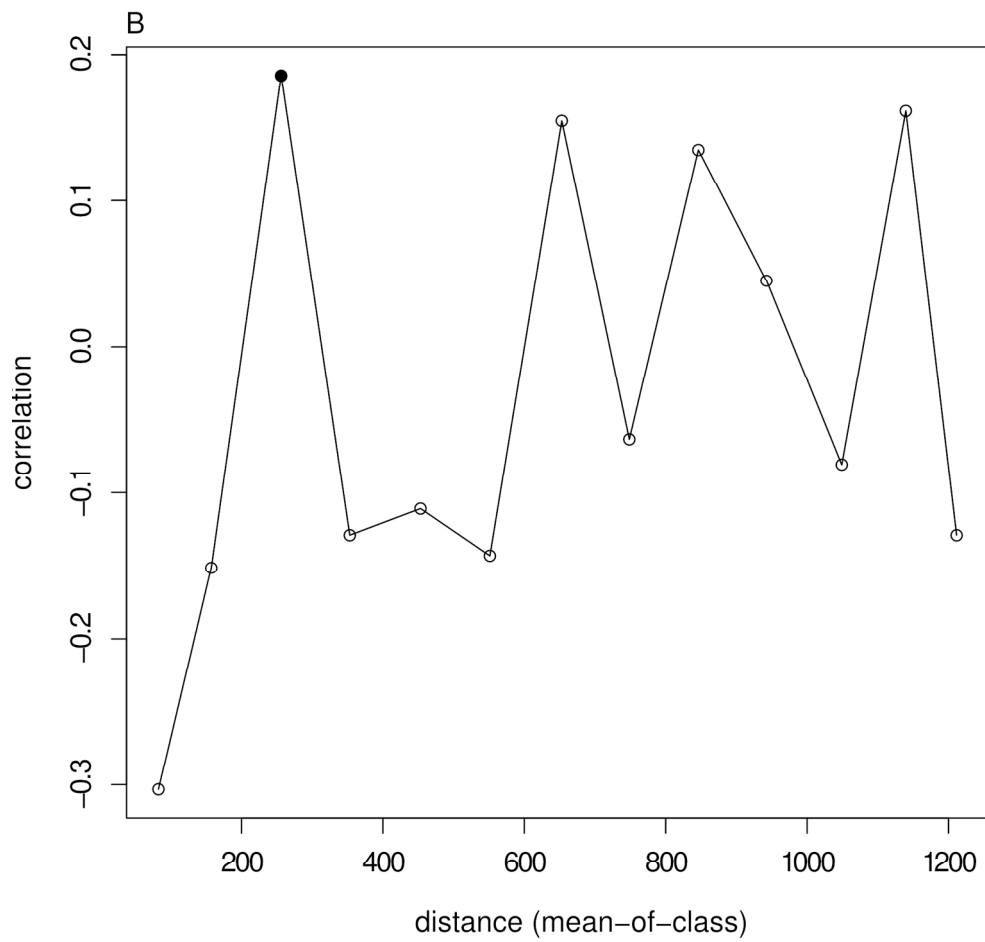


Fig. 3. *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by filled squares are significant ($P < 0.05$), open squares are non-significant
170x164mm (300 x 300 DPI)

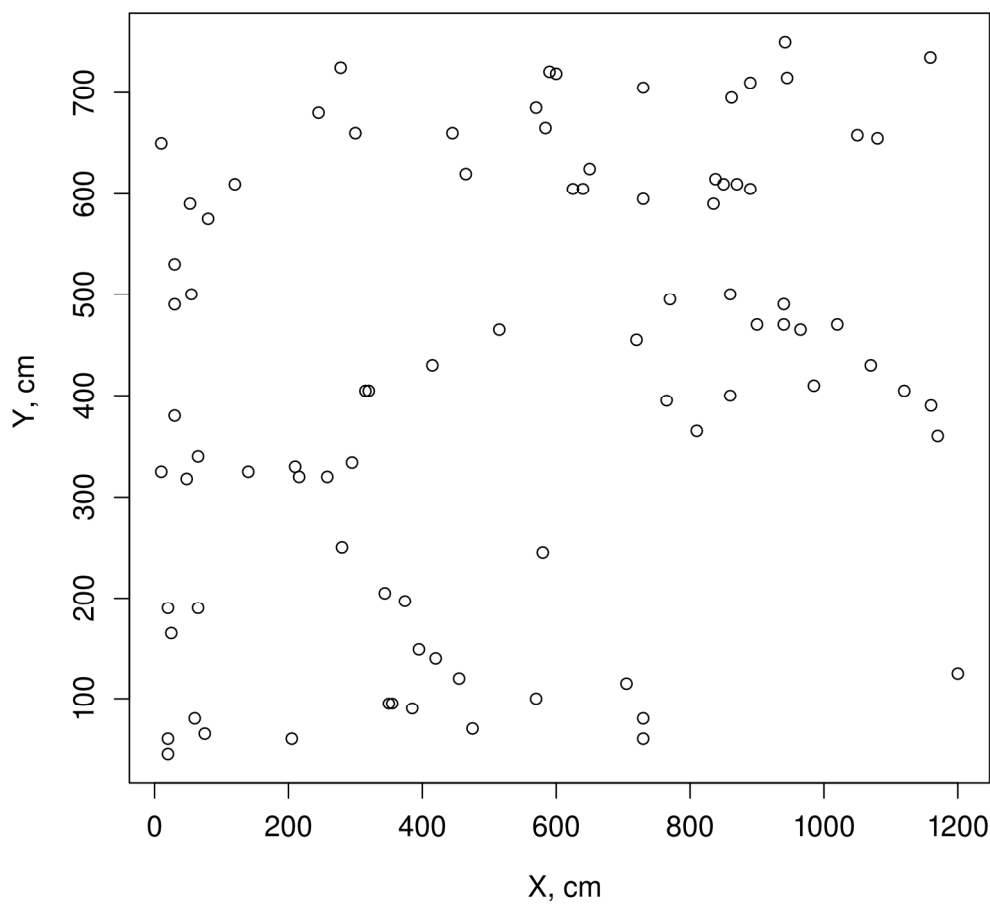


Fig. 4. Distribution of individuals of *Cerastoderma edule* within study polygon in Dalnezelenetskaya bay (2008).
170x157mm (300 x 300 DPI)



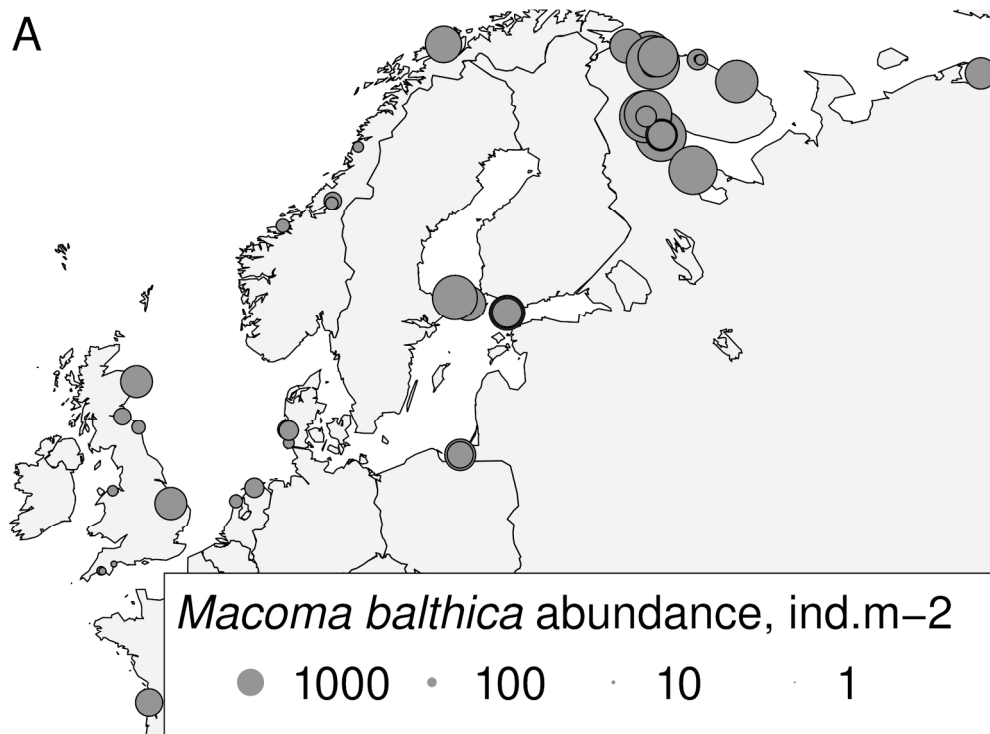


Fig. 5. Abundance distribution of *Macoma balthica* (A) and *Cerastoderma edule* (B) within the species ranges. Circles squares are proportional to mean abundance. For sources of data see Appendix A.
176x130mm (300 x 300 DPI)

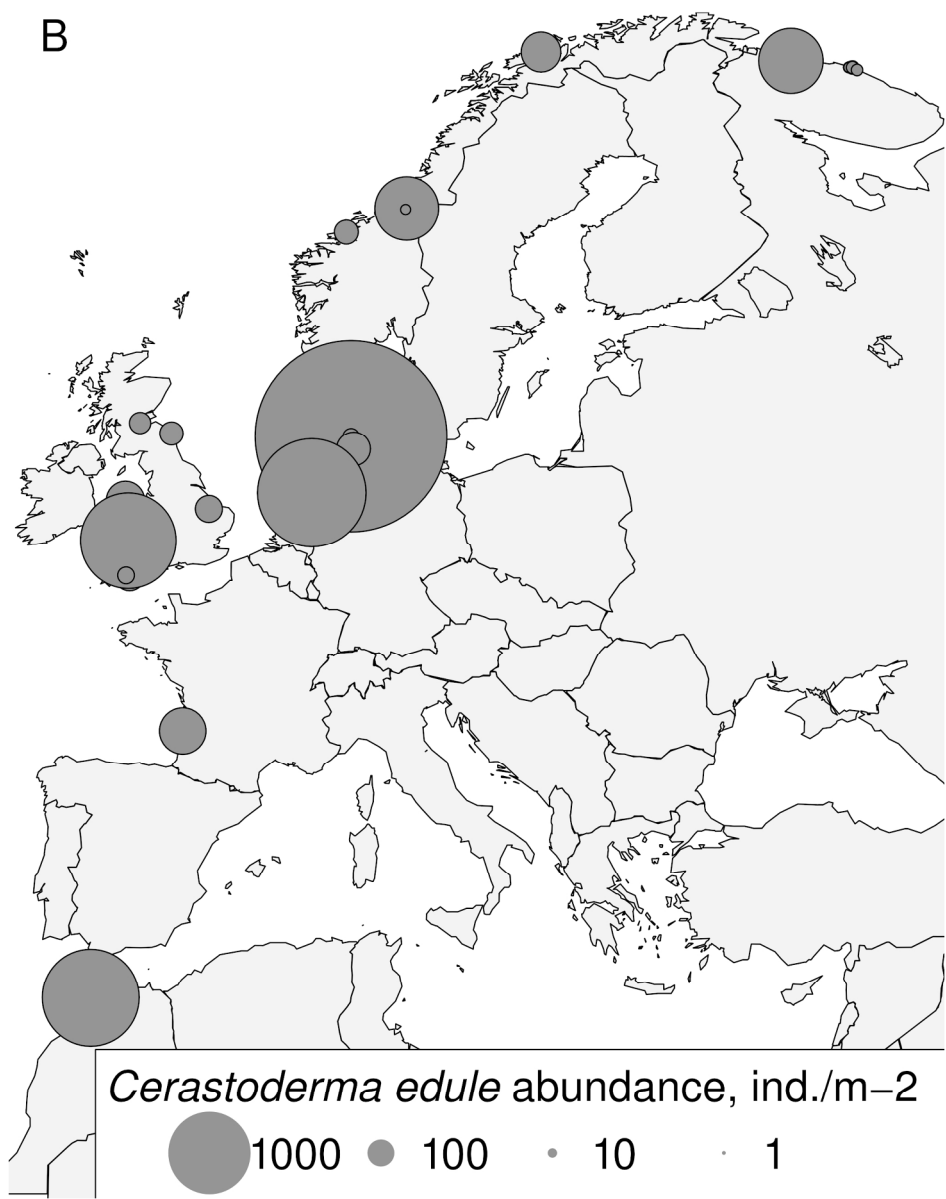


Fig. 5. Abundance distribution of *Macoma balthica* (A) and *Cerastoderma edule* (B) within the species ranges. Circles squares are proportional to mean abundance. For sources of data see Appendix A.
176x224mm (300 x 300 DPI)