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

Abstract:	Density distribution of the common infaunal bivalves, *Macoma balthica* and *Ceastoderma edule*, was studied along the Murman coast of the Barents Sea during 2002–2010. Our sampling program included two scales of abundance variability – geographic heterogenety 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<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 Macoma balthica and ramped south in Cerastoderma edule.

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1 **Abundance and spatial distribution of two infaunal bivalves — *Macoma balthica* and**

2 ***Cerastoderma edule* on the Barents Sea intertidal**

3 Sophia Nazarova[1,2,*], Evgeny Genelt-Yanovsky[1], Ksenia Shunkina[3]

4   1 – Department of hydrobiology and ichthyology, St-Petersburg State University, 16 linia

5 V.O., 29, St-Petersburg, 199178, Russia

6   2 – Department of zoology, Russian State Pedagogical University, Moyka emb., 48, St-

7 Petersburg, 191186, Russia

8   3 – Laboratory of Evolutionary Morphology, Zoological Institute RAS, Universitetskaya emb.,

9 1, St-Petersburg, 199034, Russia

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

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20 *abundance distribution across species geographic ranges revealed that both range shapes does not*

21 *match "abundant-centre" pattern, having features of ramped north in Macoma balthica and*

22 *ramped south in Cerastoderma edule.*

23   Keywords: *Cerastoderma edule*; cockle; *Macoma balthica*, Barents sea, spatial distribution,

24 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 invertabrates 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. Particulary, 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

50   abundance being near the species' limit of environmental tolerance, especially in extreme years

51   (Gaston, 2009). Since temporal variation can introduce errors in estimation of spatial abundance

52   distribution,, it is highly important to apply monitoring data series to improve the understanding of

53   differences in abundance between central and edge populations (Holt, Keitt, 2000; Johnstone,

54   Chapin, 2003). The spatial distribution and patchy structure of population density are also likely to

55   determine range limits. Edge populations usually are smaller and more spatially fragmented than

56   populations in the centre of the range (Brown et al., 1995). They may exhibit reductions in diversity

57   and in number of immigrants due to spatial arrangement only, thus resulting in an isolation-by-

58   distance effect (Sexton et al., 2009).

59   Here, we present the results of the study of abundance distribution, spatial arrangement of

60   individuals and dynamics of two intertidal bivalves *Macoma balthica* and *Cerastoderma edule* from

61   the Barents Sea, where they are expected to show controversial life history traits due to differences

62   in populations position within the species' ranges. *Macoma balthica* is no longer regarded as one

63   single species, but as a complex of Pacific *Macoma balthica balthica* and Atlantic *Macoma balthica*

64   *rubra* subspecies (Nikula et al., 2007). In Europe this complex spreads from Bay of Biscay up north

65   to the western Kara sea. Pure *M.balthica balhica* north distribution limit belongs to the Varanger

66   Peninsula, while populations in the White and Barents seas are proved to form a broad «hybrid

67   swarm» - their genetic composition is intermediate between Atlantic and Pacific forms (Strelkov et

68   al., 2007).

69   Distribution range of *Cerastoderma edule* is limited by the Barents sea in the north and by

70   Morocco Atlantic coast in the south. Cockle beds reach highest densities and biomass in the North

71   and Irish Seas, where commercial fisheries of cockles persisted for centuries (Dare et al., 2004;

72   Beukema, Dekker, 2009; Woolmer, 2010). Earlier, we proposed that *C.edule* generally follow the

73   ACH pattern across the range with a significant decline in abundance near the North-Eastern range

74   edge, but in case of successful recruitment, distinct local cockle populations in the Barents sea

75   could show much higher densities (Genelt-Yanovskiy et al., 2010). We hypothesize (1) that

76   *Cerastoderma edule*, as a temperate-zone species, will demonstrate lower densities of individuals at

77   the range edge and scattered distribution of local populations across the Murman shore of the

78   Barents sea as in comparison to *Macoma balthica*, and (2) non-random density distribution of

79   individuals within the local populations on most of tidal flats for both species.

80   MATERIALS AND METHODS

81   **Study area**

82   Murman coast is a northern border of the Kola Peninsula with a coastal line length of about 700 km,

83   including numerous bays and fiords. The longest, Kola Bay, divide Murman coast into two regions:

84   Western Murman and Eastern Murman. These two parts demonstrate different environmental

85   conditions, as the effects of Gulf Stream drop sharply from west to east. After E.F. Gourjanova,

86   I.G. Zaks and P.V. Ushakov (Gourjanova & Ushakov, 1929; Gourjanova et al.,1929; Gourjanova et

87   al., 1930) we consider Western Murman, Kola inlet and Eastern Murman as tree distinct regions.

88   Owing to gradient changes in environment this whole area has transitional biogeographical status -

89   from boreal to arctic zone (Zenkevich, 1963).

90   **Sampling**

91   We used two different quantitative sampling procedures to resolve all the given problems: (i)

92   random sampling for evaluation of mean abundance across Murman coast and (ii) regular grid

93   small-scale sampling aimed to analyze the spatial arrangement of bivalve densitiy

94   (microdistribution) within the tidal flats. All samples were sieved through 1 mm mesh.

95   I. Random sampling was conducted at 18 sites (all for *C. edule* and 12 of them for *M.*

96   *balthica)* (table. 1). The sampling took place in July–August, from 2002 to 2010. We took five

97   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 m^{-2} at the sites inhabited by *Macoma* alone, and with area of 1/10 m^{-2} for sites where

99   *Macoma* 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 x 7.5 m) was divided into twelve equal sectors. From each sector

106   three sediment cores (1/30 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 x 7.5 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.

123   Spatial patterns were investigated with correlograms based on Moran's spatial autocorrelation

124   coefficient, I(g) (Sokal, 1979, Bjornstad, 2013). Samples within sites were grouped according to

125   distances, estimated directly from the differences in cartesian coordinates. To calculate Moran's I(g)

126   we sorted samples into distance classes of 1 m. The null hypotheses of I(g)=0 were checked with

127   permutation test. Thus we clarified the nature of patterns and estimated patch sizes.

128   We tested both vertical and horisontal spatial gradients of abundance across the shore using

129   Kendall's rank correlations (Hollander, Wolfe, 1973).

130   All calculations were done with R (R-core, 2014). In all cases, statistical significances were

131   tested at 5% probability level.

132   RESULTS

133   **Bivalve abundance at the Murman coast of the Barents Sea**

134   The abundance of *M. balthica* at the sites taken at the West Murman and Kola Bay varied from

135   hundreds to thousands individuals per square meter. Maximum abundance (more than 3000 ind. m$^-$

136   ^{2}) was observed in Kola Bay at Cape Abram site. At the East Murman *M. balthica* abundance was

137   significantly lower (less than 100 ind. m^{-2} at the most sites). The lowest abundance (about 30 ind.

138   m^{-2}) was observed in Dalne-Zelenetskaya bay (East Murman) (figure 1, A). It was also shown that

139   *M. balthica* mean abundances were significantly different at three regions of the Murman coast

140   (Kruskal-Wallis test: $\chi 2 = 17.6$, $p < 0.0001$).

141   Alive individuals of *C. edule* were revealed only at 11 sites out of 18. We ~~haven't~~ found any

142   alive individuals at bays Klimkovka, Dolgaya, Tyuva, Gavrilovo, Drozdovka, Ivanovskaya and

143   Gremikha. The highest abundance of cockles were found at Ura-bay, West Murman (282±68

144   indd./m^{-2}) (figure 1, B). The other site with rather high abundance was found also in the Western

145   Murman region – it was Pala-bay, West Murman (45±9 ind. m^{-2}). In 2007 cockle abundance at this

146   site decreased to 10 ind .m^{-2}. Cockle abundance was notably lower at all other sites (less then 10

147 ind. m^{-2} at most sites) (figure 1, B). Mean abundance at the West Murman was significantly higher

148 than at other two regions. (Kruskal-Wallis test: $\chi 2 = 21.4$, $p < 0.001$).

149   At sites Pechenga, Ura, Retinskoe, Bolshaya Volokovaya we have found only a few empty

150 shells in cores, but searching out of sampling areas some alive individuals were found. At some

151 sites (Gavrilovo, Drozdovka) we have found only empty shells of *C. edule*. Shelpino population

152 completely become extinct after 2009.

153 **Microdistribution**

154 No spatial patterns were found for *M. balthica* in Dalne-Zelenetskaya bay in 2007. Thus, we

155 supposed that probably the sample site size could be too small, so it was 2 times enlarged in 2008.

156 After that we found that significantly positive Moran's I was for lag 1.5–2 m and significantly

157 negative for lag 4 m (figure 2, B). It allows to suppose that there could be small *Macoma* patches

158 (diameter was equal to the core diameter, $1/30$ m^{-2}) that aggregate to a larger one.

159   No spatial patterns for *Macoma* were found in Yarnyshnaya bay in 2008. At Pala bay patches

160 with diameter about 2–4 m were found (figure 2, A). Series of negative significant Moran's I may

161 indicate a gradient distribution at this site. According to the Kendall test we conclude that there was

162 abundance gradient towards a freshwater stream crossing the intertidal zone ($\tau = 0.55$; $p < 0.0001$).

163   As *Macoma* abundance in Pala bay was rather high, we were able to investigate spatial

164 distribution of molluscs of different age groups (table 2). A horizontal gradient was revealed for

165 clams aged 2+, 3+ and 5+. Elder *Macoma* were aggregated in big patches with diameter about

166 several meters. The abundance of the oldest individuals was low, their distribution pattern was

167 evaluated as random.

168   For *C.edule* we found aggregation patches only in Yarnyshnaya and Pala bays. Patch

169 diameter was about 3 meters in Yarnyshnaya bay (figure 3, B), and in Pala bay at investigation

170 polygon there was only one huge aggregation with diameter about 5 meters (figure 3, A). At Dalne-

171 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,

197 2013). According to our data, mean *Macoma* abundance was significantly lower in East Murman

198 sites in comparison to West Murman and Kola Bay sites. At West Murman and in Kola Bay clam

199 densities are comparable with their densities in the White Sea, in the Baltic Sea and in the nearest

200 waters – the northern part of the Norwegian Sea (for example Semenova, 1974; Aschan, 1988;

201 Bostrom, Bonsdorf, 2000; Oug, 2001; Varfolomeeva, Naumov, 2013; Rousi et al., 2013;

202 Gerasimova & Maximovich, 2013). At the East Murman *Macoma* abundance is lower than in the

203 other regions. We found similar abundances in the south part of the Norwegian sea and in the

204 Wadden Sea (Sneli, 1968; Beukema, 1976; Jensen, Jensen, 1985; Reise et al., 1994).

205   This difference could be interpreted by difference in general environmental conditions

206 between West and East Murman. West Murman is an area of numerous fjord-like bays, among

207 which Kola Bay is the longest (57 km) and Pechenga and Ura are more typical – 16 and 19 km long

208 respectively. East Murman coast contrary is comparatively straight. Also, western current, a branch

209 of Gulf Stream, dominates the nearshore hydrodynamics in East Murman, while longer bays of

210 West Murman are more isolated and thus provide more stable conditions (Denisov & Dzhenyuk,

211 1995).

212   Regional heterogeneity was declared even within West Murman and Kola Bay (figure 1A).

213 Among all sites, the highest density was recorded in the inner part of the Kola Bay – in Cape Abram

214 site (figure1). Nagornoe, nearest to Cape Abram site, situated on the opposite shore of Kola bay,

215 demonstrated lower clam density. We suppose that lower abundances in Nagornoe could be a

216 consequence of its location nearby to the sewer outlet of city of Murmansk. It is well known, that

217 *Macoma* uses two types of feeding modes – suspension-feeding, more typical for clams living on

218 sandy bottoms, and deposit-feeding which is usual for *Macoma* from muddy habitats (Olaffson,

219 1989). Despite we didn't conducted organic content and grain-size analysis for Cape Abram and

220 Nagornoe sites, it is obvious that the tidal zone around sewer outlets (Nagornoe) contains additional

221 amounts of silt as compared to background values (Littler & Murray, 1975; de-la-Ossa-Carretero et

222   al., 2012). Thus, in muddy habitats, such as Nagornoe, *Macoma* shows density-related effects due

223   to intraspecific competition for food and space, at least on growth levels (Olaffson, 1989).

224

225   Densities of *M.balthica* in Ivanovskaya, the easternmost site for this species in our dataset,

226   were dissimilar with other East Murman localities, because in this site *Macoma* appeared to be more

227   subtidal than intertidal species – it occurs just below the LWL. Subtidal *Macoma balthica*

228   population was previously reported in the Pechora sea (SE part of the Barents sea) with mean

229   densities of 654 ind./m^{-2}, which is twice lower than in Ivanovskaya (Denisenko et al., 2003).

230   Our data suggest that *Macoma balthica* abundance distribution within the species range does

231   not clearly follow the "abundant centre" (figure 5, A) and is more likely a "ramped north" (for

232   names of distribution shapes see Sagarin & Gaines, 2002). Surprisingly, mean adult (>1 mm)

233   *Macoma* densities in West Murman local populations were more similar to the White and Baltic

234   Seas, and were higher than long-term mean values available for North Sea and Bay of Biscay (see

235   appendix A). This result corresponds with the distribution of Atlantic *Macoma balthica rubra* and

236   Pacific *Macoma balthica balthica* lineages in Europe (Nikula et al., 2007; Strelkov et al., 2007).

237   European Atlantic *M.b.rubra* inhabits North Sea and Northeast Atlantic coasts, while *M.b.balthica*

238   occurs together *M.b.rubra* in the Baltic and northern marginal seas and is regarded as a result of

239   trans-Arctic invasion in early Holocene (Nikula et al., 2007).

240   Mean densities of adult *Cerastoderma edule* on the Murman coast of the Barents Sea, varying

241   in most sites around 10 ind. m^{-2} were generally lower than in other parts of the species range

242   (Beukema, 1989; Ivell, 1989; André, Rosenberg, 1991; Bachelet et al., 1992; Ramon, 2003; Dare et

243   al., 2004). Very similar to the Barents Sea cockle density was previously reported from Tromsø,

244   North Norway (Oug, 2001). That data also supports hypothesis that low abundance is typical feature

245   of the northern part of the species range. *Cerastoderma edule* abundance distribution pattern within

246   the range could be named as "abundant centre" (figure 5, B). Takimg into account that at

247 southernmost distribution limit, Merja Zerga (Morocco), cockle density may reach 1200 ind. m^{-2}

248 with long-term mean of 638 ind. m^{-2} , abundance pattern could be probably transitional between

249 typical "abundant centre" and "rumped south", because (Gam et al., 2010).

250   Current easternmost *Cerastoderma* local population is located in Trashina bay (~68° 59' N,

251 ~36° 30' E), we didn't find any alive cockles further east. However, in Drozdovka bay (~100 km

252 east from Trashina) we've found out two non-fossilized cockle shells, which means that temporary

253 outbreak settlement of this species occurred here some years ago. Murman coast clearly is a

254 dynamic range edge for *Cerastoderma*, and thus in five other sites (Pechenga, Retinskoe, Tuva,

255 Bolshaya Volokovaya, Gavrilovo) there was no possibility to estimate cockle density using standard

256 sampling methods and only shells were found. No cockles were also found in the inner part of the

257 Kola Bay, Cape Abram and Nagornoe (figure 1,B). We suppose that it could be explained by known

258 sensitivity of *Cerastoderma* to pollution load (Savari et al., 1989), which should be significant near

259 the city and port of Murmansk, largest coastal industrial area in the Barents Sea region.

260   *Cerastoderma edule* population dynamics has a very typical feature of periodically occurring

261 mass mortality events, when adult densities sharply reduces from thousands of individuals to single

262 cockles per square meter due to a variety of factors. After that slow population recovery takes place

263 (Strasser at al., 2001; Malham et al., 2012; Callaway et al., 2013). In the Wadden sea during

264 periods, called after Ducrotoy et al. (1991) as "recovery", cockle density may reach 54000 ind. m^{-2}

265 including individuals of all age groups (Malham et al., 2012). According to our study,

266 *Cerastoderma* local population in Ura bay on West Murman unambiguously had features of

267 recovery phase of population dynamics in 2010 after "crisis" phase observed in 2005 (figure 1, B).

268 During our first visit, only solitary individuals were found across the tidal flat, while in 2010 mean

269 cockle density was 282 ind. m^{-2}, which is highest density value for the Barents sea. Our results on

270 cockle local population recovery in Ura bay support the dependence of Barents sea populations of

271 invertebrates and pelagic fish on larval drift from west (Gjøsaeter, 1995; Mikkelsen & Pedersen,

272   2004; Strelkov et al., 2007).

273   Spatial aggregation may form on different scales. It could be observed at geographic

274   distribution level, where distribution of populations and their abundance is a response of availability

275   of suitable habitats, or simply could be driven by patchy structure of the biotope, which is critically

276   important for distribution of individuals (Thrush et al., 1989; Kraan et al., 2010; Santos et al.,

277   2012). Remarkably low *Cerastoderma* and *Macoma* densities in East Murman local populations

278   provoked a further study of abundance distribution of these species within the tidal flats. Since the

279   beginning it was obvious that cockles have non-random distribution during low tides, as the

280   sampling of qualitative material for our previous study on dynamics and growth of *Cerastoderma*

281   *edule* (Genelt-Yanovskiy et al., 2010) usually became easy right after the first mollusk was

282   discovered, even in bays where quantitative estimation of density was not possible.

283   Our data show that spatial distribution patterns of *Cerastoderma* and *Macoma* were site-

284   specific. Most significant non-random distribution of *Macoma* was observed in Pala bay, where

285   density of smaller individuals gradually increased towards the streambed flowing through the

286   central part of tidal flat, bigger clams formed broad patch and oldest individuals were arranged

287   randomly (figure 2,A, table 2). Gradient pattern in younger *Macoma* is probably determined by

288   higher availability of dissolved organic matter brought by the stream and thus lower competition

289   with uniformly distributed adults.

290   *Cerastoderma* distribution on the Pala bay intertidal as well as in Yarnishnaya bay was also

291   non-random, but cockle formed patchy aggregations 3–5 meters in diameter (figure 3,B).

292   Experimental data suggested that the high abundance causes more uniform distribution of

293   *Cerastoderma* individuals, but when density is low, cockles become more randomly distributied

294   (Richardson et al., 1993). *Cerastoderma* is highly mobile species; each individual can crawl over

295   0.5 m during each tidal cycle, and thus distribution pattern changes over time (Richardson et al.,

296   1993). In the Wadden sea, where *Macoma* and *Cerastoderma* may form patches with the size over

297 200 and 1000 meters respectively (Santos et al., 2012). In Dalne-Zelenetskaya bay cockles showed

298 random distribution pattern at the chosen scale. Further attempt of individual location of cockles

299 within the polygon revealed that even at low densities (figure 4), typical for the East Murman,

300 cockles could be arranged uniformly within tens of meters.

301 Intertidal infaunal bivalves, inhabiting same area may demonstrate similar patterns of spatial

302 distribution over tidal flats (Kraan et al., 2010; Santos et al., 2012). Within the present study we

303 didn't evaluated abundance of the *Mya arenaria,* third infaunal bivalve species occur on the tidal

304 flats of the Barents Sea, but more abundant in the White Sea (Gerasimova, Maksimovich, 2013).

305 Sand gapers were observed in most sites where abundances of *Macoma balthica* and *Cerastoderma*

306 *edule* were estimated, but only random distribution pattern was typical for *Mya*.

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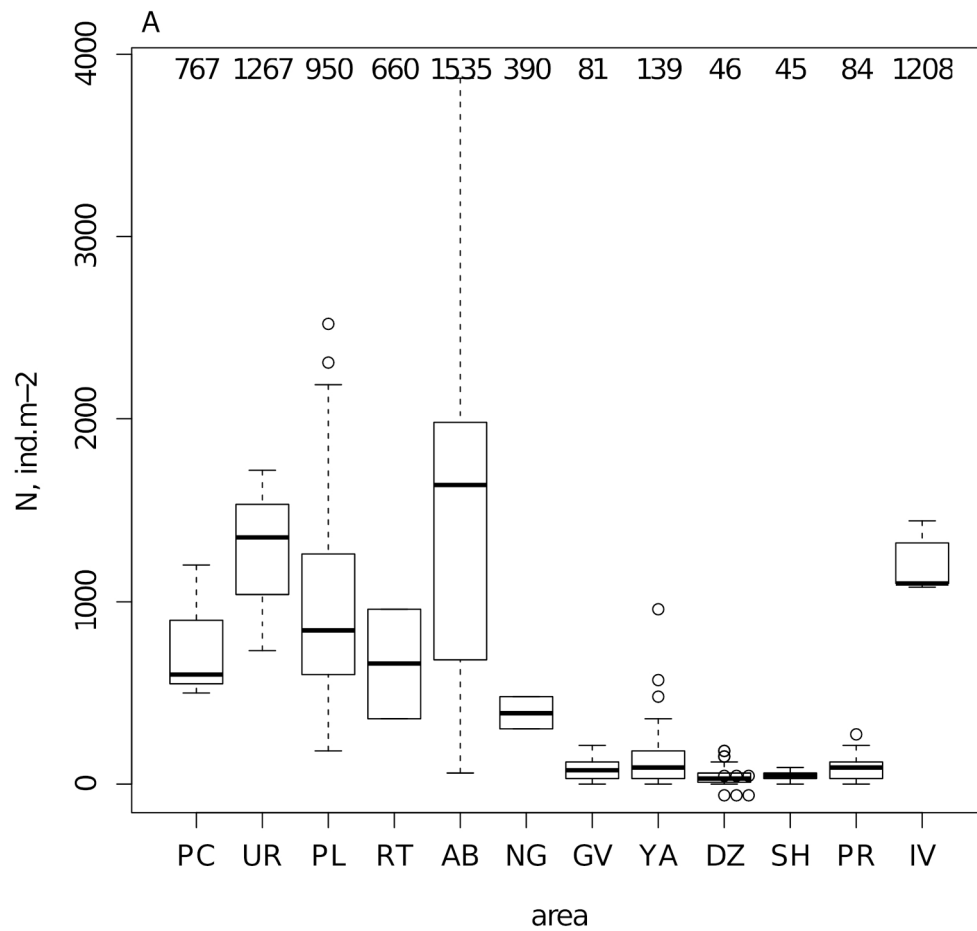
483   **Fig. 1.** Mean abundance (N, ind.m^{-2}) of *Macoma balthica* (A) and *Cerastoderma edule* (B) in

484   the Barents sea. Samples are arranged from West to East. At the box-plots box marked Q1, median

485   and Q3, whiskers marked 1.5 IQR. Mean abundance indicated at the top.

486   **Fig. 2.** *Macoma balthica*. Spatial correlograms, based on Moran's Autocorrelation Coefficient

487   I, for Pala (A) and Dalnezelenetskaya (B) bays. Autocorrelation coefficients represented by filled

488   squares are significant (P< 0.05), open squares are non-significant

489   **Fig. 3.** *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation

490   Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by

491   filled squares are significant (P< 0.05), open squares are non-significant

492   **Fig. 4.** Distribution of individuals of *Cerastoderma edule* within study polygon in

493   Dalnezelenetskaya bay (2008).

494   **Fig. 5.** Abundance distribution of *Macoma balthica* (A) and *Cerastoderma edule* (B) within

495   the species ranges. Circles squares are proportional to mean abundance. For sources of data see

496   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
East Murman	Klimkovka	69.23, 34.64	2009
	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.
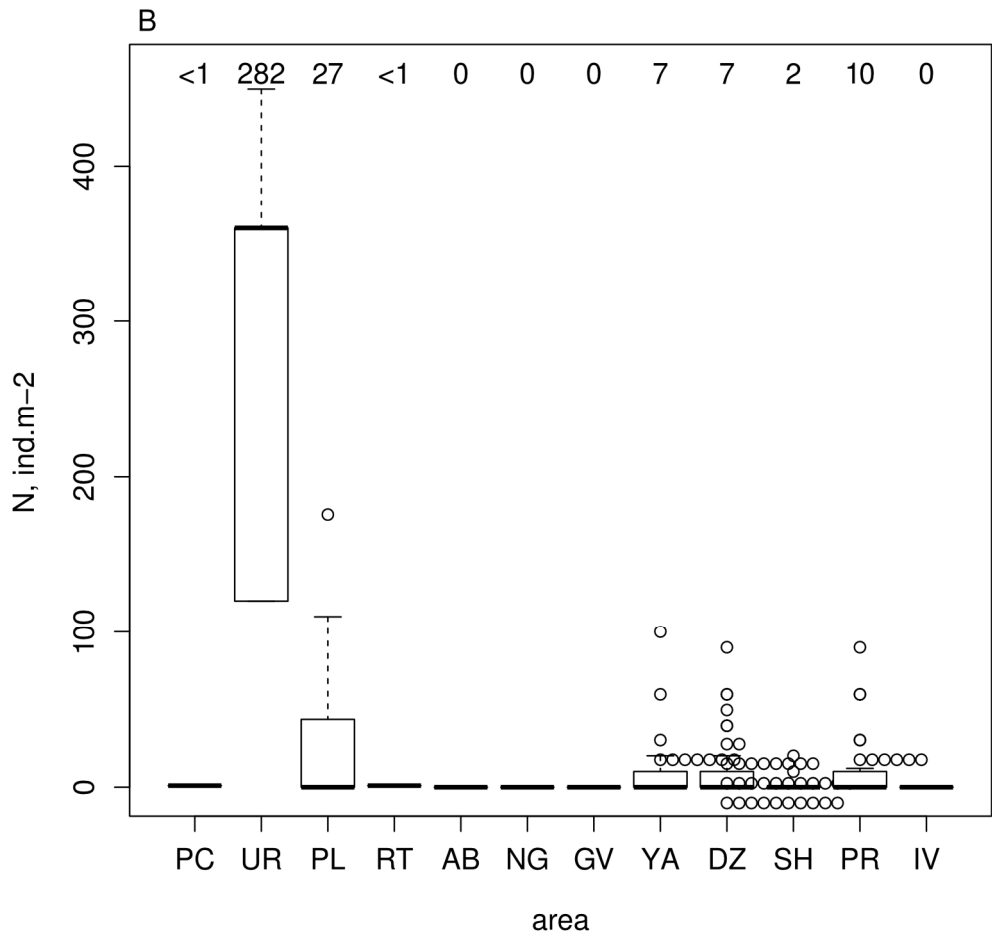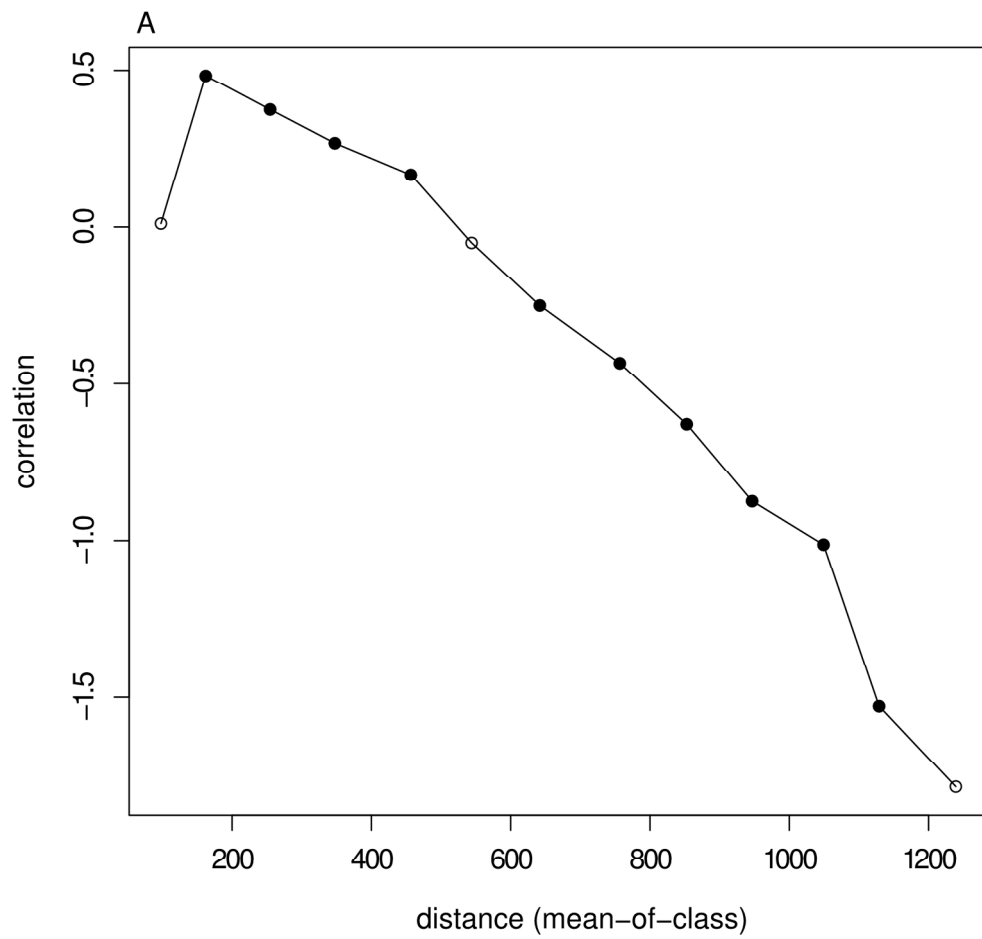171x161mm (300 x 300 DPI)

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.
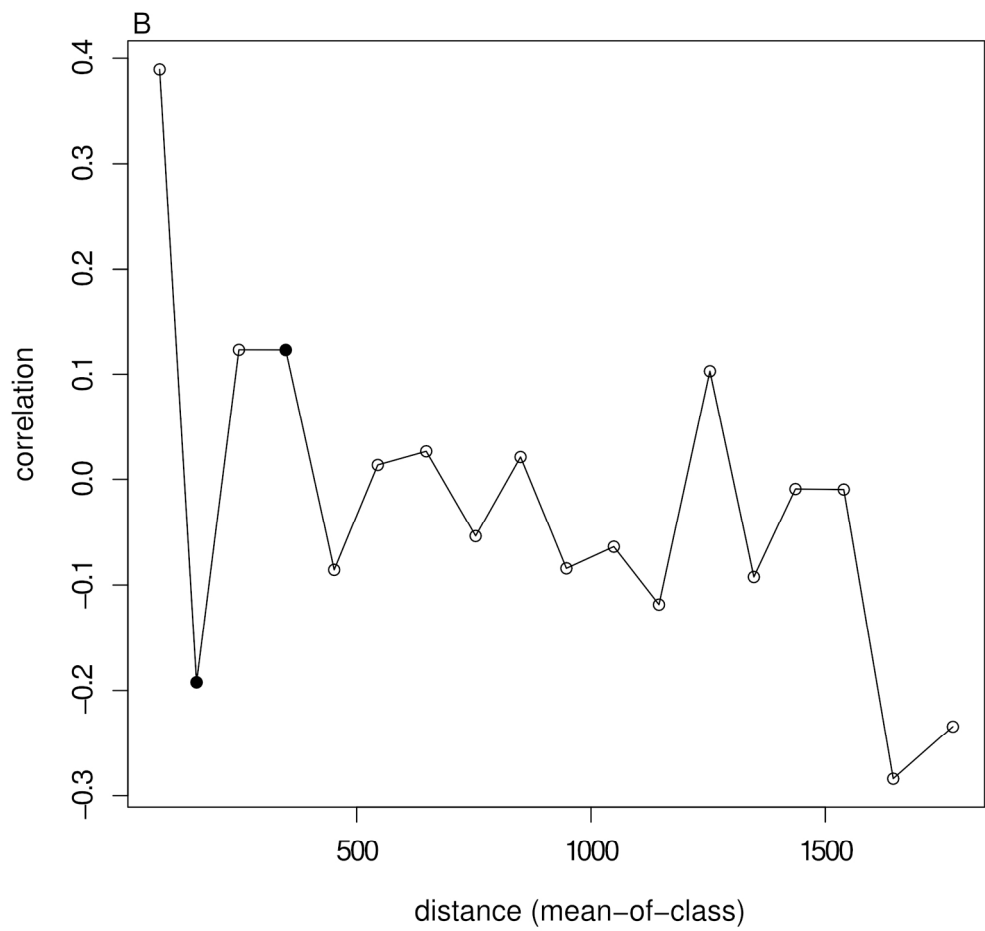170x161mm (300 x 300 DPI)

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 analisys Moran's I spatial

correlograms and gradient analisys 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%.
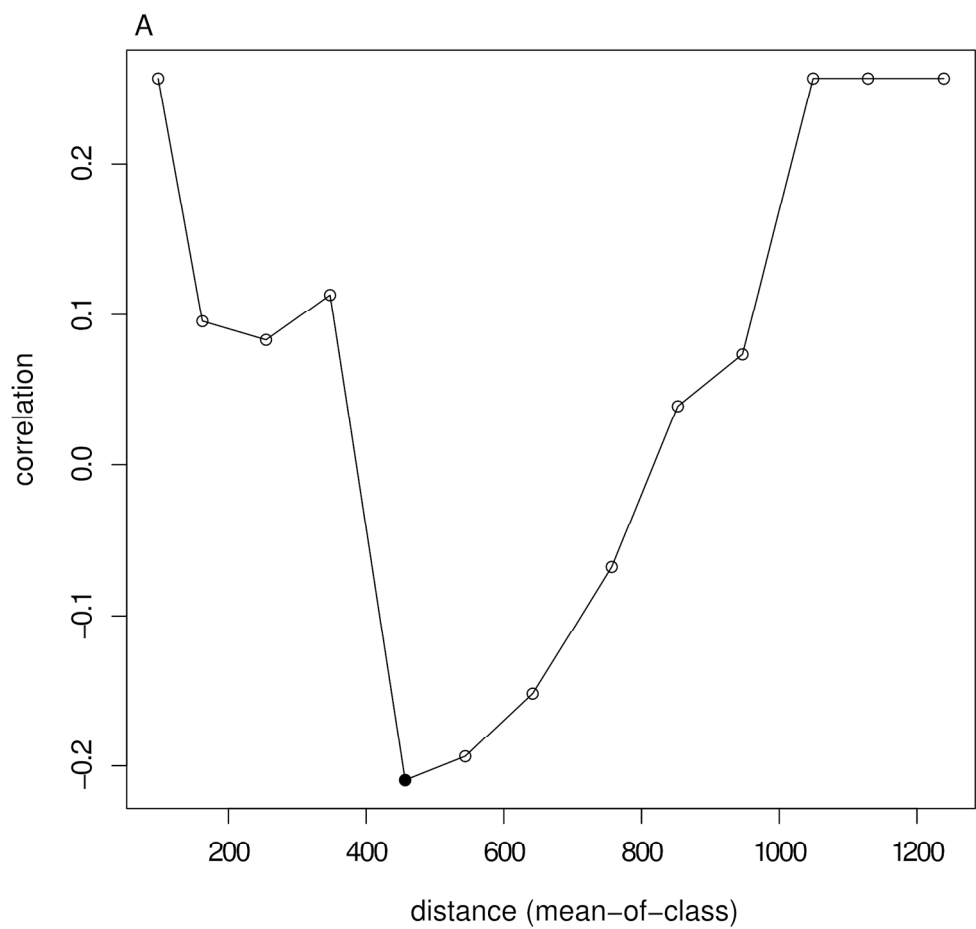
Fig. 3. *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by filled squares are significant (P< 0.05), open squares are non-significant
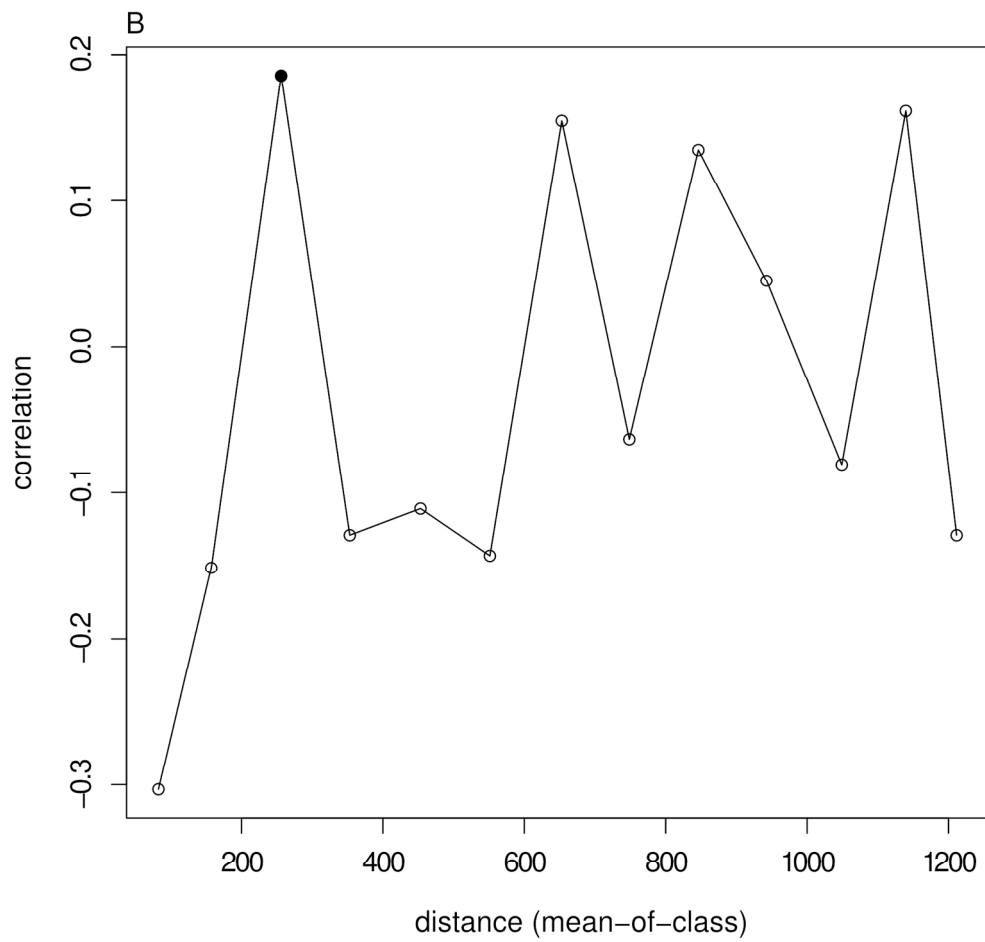172x165mm (300 x 300 DPI)

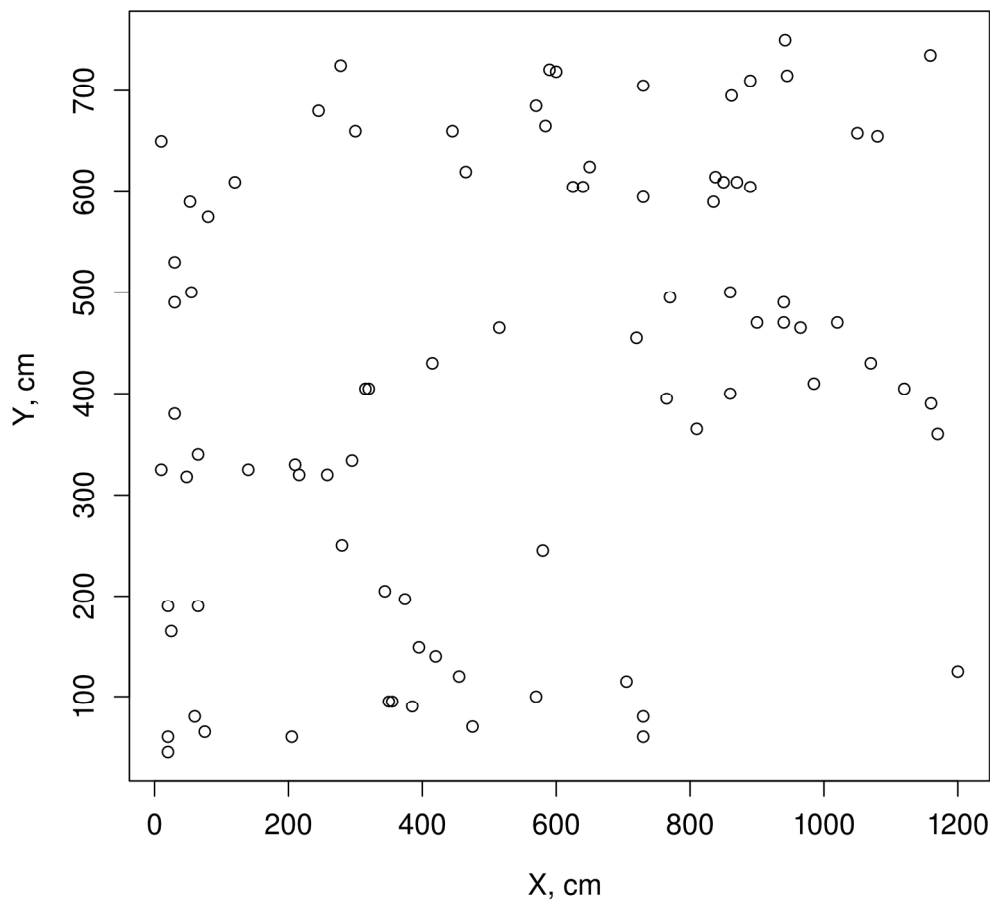**Fig. 3.** *Cerastoderma edule*. Spatial correlograms, based on Moran's Autocorrelation Coefficient I, for Pala (A) and Yarnishnaya (B) bays. Autocorrelation coefficients represented by filled squares are significant (P< 0.05), open squares are non-significant
170x164mm (300 x 300 DPI)

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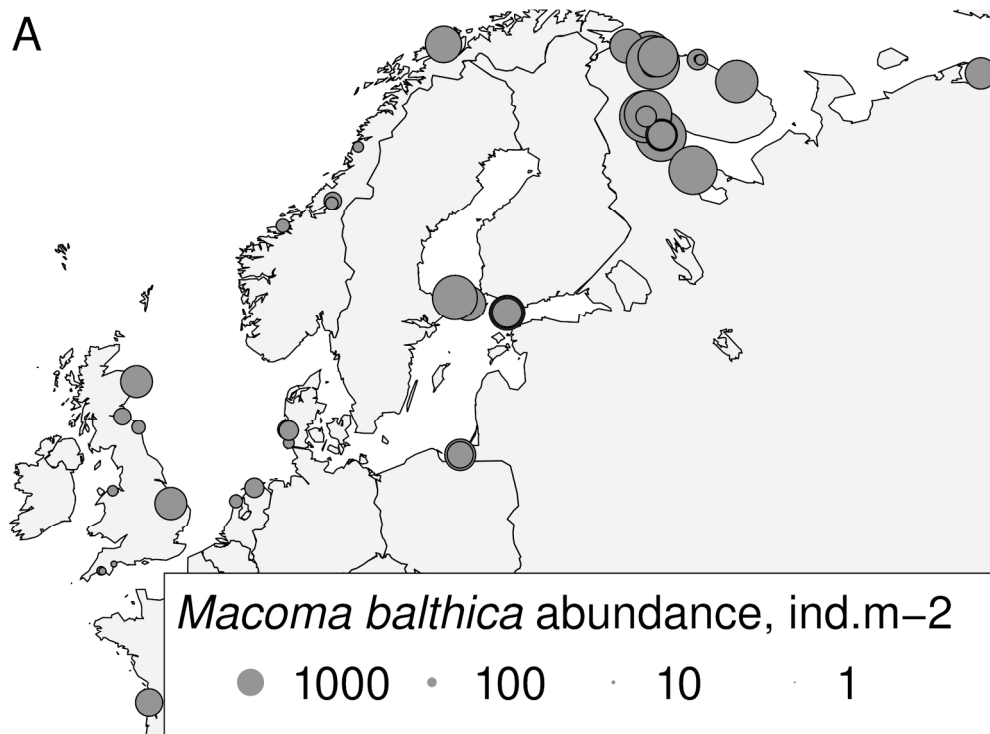*170x157mm (300 x 300 DPI)*

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.
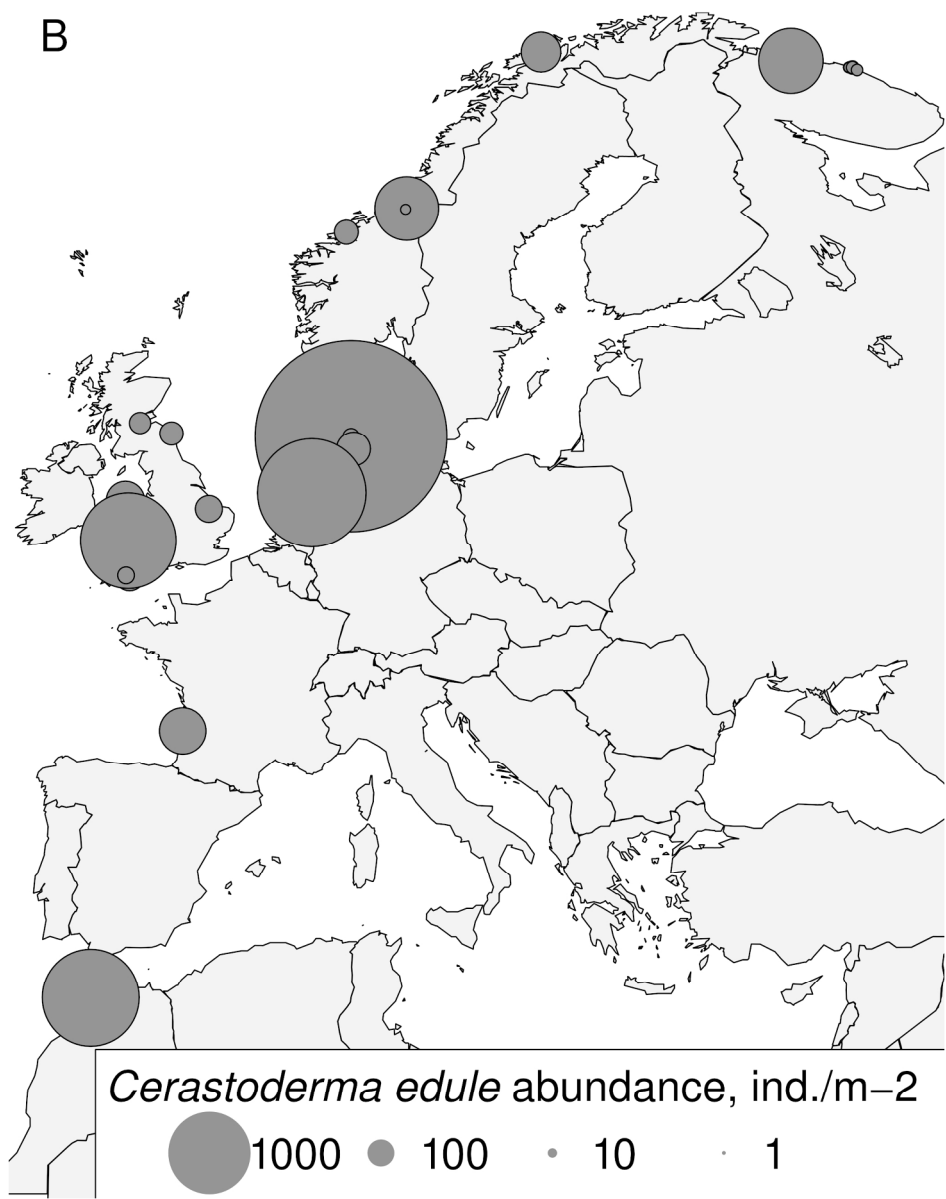176x130mm (300 x 300 DPI)

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)