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Abundance distribution patterns of intertidal bivalves *Macoma balthica* and *Cerastoderma edule* at the Murman coast tidal flats (the Barents Sea)

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1   INTRODUCTION

2   Patterns of species' abundance at the biogeographic extremes may provide insights into such

3   essential issues in ecology as identification of borders between adjacent biogeographic regions

4   and causes of species range limits. Large-scale distribution of species abundance is also a key

5   element of applied sciences such as planning of protected areas and designation of species into

6   regional Red Lists. A widespread paradigm, known as "abundant-centre hypothesis" (ACH) is

7   widely used to test whether the highest species abundance belongs to the range centre and

8   declines towards range edges (Sagarin et al., 2006). Intertidal fauna is an ideal test system for

9   studying latitudinal gradients. In Western Europe, many intertidal and high subtidal marine

10   invertebrates have extended ranges with distinct north (or north-eastern) and south (or south-

11   western) limits characterized by diametrically opposed combination of environmental conditions.

12   Recent studies on wide-spread marine coastal invertebrates have shown that abundance centre

13   pattern does not apply to most species equally, and even closely related species could show

14   different spatial patterns (Sagarin & Gaines, 2002; Rivadeneira et al., 2010).

15   Empirical approaches to quantify abundance in different parts of the range vary widely. One of

16   the main challenges for examining the abundant centre pattern is a logistical difficulty of

17   sampling throughout the whole species range. Particularly, it could be a problem to get adequate

18   samples from the range edge, where local populations are not stable in time and can

19   spontaneously become extinct and later reoccupy suitable habitats (Sagarin & Gaines, 2002;

20   Sexton et al., 2009).

21   Species ranges are not stable in time, often shifting, expanding and contracting (Gaston, 2009).

22   Fluctuations of environmental variables, such as climate oscillations, may alter population fitness

23   at the distribution limits and range shifts can lag behind environmental changes (Pfenninger et

24   al., 2007; Svenning et al., 2008). Marginal populations exhibit greater temporal variability in

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

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

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

28   of differences in abundance between central and edge populations (Holt & Keitt, 2000;

29   Johnstone & Chapin, 2003). The spatial distribution and patchy structure of population density

30   are also likely to determine range limits. Edge populations usually considered to be smaller and

31   more spatially fragmented than populations in the centre of the range (Brown et al., 1995). They

32   may exhibit reductions in diversity and in number of immigrants due to spatial arrangement only,

33   thus resulting in an isolation-by-distance effect (Sexton et al., 2009).

34   Here, we present the results of the study of abundance distribution of *Macoma balthica* and

35   *Cerastoderma edule,* two key bivalve species at the tidal flats of the Barents Sea. *Macoma*

36   *balthica* is currently regarded as a complex of Pacific *Macoma balthica balthica* and Atlantic

37   *Macoma balthica rubra* subspecies (Nikula et al., 2007). In Europe this complex spreads from

38   Bay of Biscay up north to the western Kara sea (Figure 1 A). Southern distribution range limit of

39   *Macoma* has shifted several hundreds of kilometres north during last decades (Beukema et al.,

40   2009). Pure *M. balthica balhica* northern distribution limit belongs to the Varanger Peninsula,

41   while populations in the White and Barents seas are proved to form a broad "hybrid swarm" -

42   their genetic composition is intermediate between Atlantic and Pacific forms (Strelkov et al.,

43   2007). *Cerastoderma edule* range is shaped into at least two genetically different groups of

44   populations along the North Atlantic coast, but separation between these groups does not have a

45   subspecies level (Krakau et al., 2012). Earlier we suggested that low density of individuals is

46   typical for *C. edule* in the Barents Sea, a North-Eastern distribution limit for the species (Genelt-

47   Yanovskiy et al., 2010)(Figure 1A). To study latitudinal clines in geographical abundance

48   distributions, we put together published records of mean *M. balthica* and *C. edule* density across

49   species' European ranges with our own observations from the Barents Sea.

50   MATERIALS AND METHODS

51   **Study area**

52   Murman Coast is a northern border of the Kola Peninsula with a coastal line of about 700 km,

53 including numerous bays and fjords. The longest among them, Kola Inlet, divide Murman Coast

54 into two regions: Western Murman and Eastern Murman. Murman environmental conditions are

55 determined by westerly warm Murman Coastal Current (Denisov & Dzhenyuk, 1995).

56 Interaction between Murman Coastal Current and Arctic water backflow causes remarkable

57 cooling gradient from West to East Murman. Owing to gradient changes in environment this

58 whole area has transitional biogeographical status – from boreal to arctic zone (Zenkevich,

59 1963). After E.F. Gourjanova, I.G. Zaks and P.V. Ushakov (Gourjanova & Ushakov, 1929;

60 Gourjanova et al.,1929; Gourjanova et al., 1930) we consider Western Murman, Kola Inlet and

61 Eastern Murman as three distinct regions of Murman Coast.

62 **Sampling**

63 Samples were collected at 18 sites across the Murman Coast (all for *C. edule* and 12 of them for

64 *M. balthica)* (Figure 1, table 1). The sampling took place in July–August, from 2002 to 2010. At

65 sites inhabited by *Macoma* alone, 5 cm deep cores with a surface area 0.03 m^2 were taken; for

66 sites where *Macoma* and *Cerastoderma* occurred together, 0.1 m^2 corers were used. All samples

67 were sieved through 1 mm mesh. Each soft-bottom tidal level was characterized with five

68 samples at all sites studied.

69 All collected bivalves were sorted, identified and counted. Shell length of each individual was

70 measured using calipers to the nearest 0.5 mm. Age of individuals was determined by counting

71 annual growth marks on outer side of the shell. This method of age estimation was used basing

72 on previous studies on *Macoma* and *Cerastoderma* in the region, confirming that structural

73 marks on shells of the molluscs in the subarctic seas reflect the annual growth patterns, due to

74 the strong seasonal variation in sea water temperature (Agarova, 1979; Maximovich et al., 1992;

75 Maximovich & Gerasimova, 2004, Nazarova et al, 2010).

76 **Statistical analysis**

77 Similar statistical procedures were employed for both species. We started with describing the

78 abundances from each site. We used both medians and means as measures of central tendency

79   and created Tukey boxplots (Tukey, 1976) to illustrate abundance variability. Data on abundance

80   from individual samples from one site was used for plotting. Also year-to-year variability of

81   mean abundance and size-frequency distributions of the species were analysed. Kruskal-Wallis

82   test (Hollander, Wolfe, 1973) was used to compare regional average abundances. The data from

83   published records of mean *C. edule* and *M. balthica* abundance are presented together with our

84   own observations in two maps (Figure 5). For the comparisons we used only mean densities of

85   bigger than spat-sized individuals of *Macoma* and *Cerastoderma*. Full details on all papers used

86   in assessment of global distribution patterns are listed in electronic supplementary (appendix A).

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

88   tested at 5% probability level.

89   RESULTS

90   The abundance of *Macoma balthica* at Western Murman and Kola Inlet sites varied from

91   hundreds to thousands individuals per square meter. *M. balthica* mean density was significantly

92   different at three regions of the Murman coast (Kruskal-Wallis test: $\chi^2 = 17.6$, $p < 0.0001$).

93   Highest mean *M. balthica* density (3350 ± 520 ind. m^{-2}) was observed in 2005 at Cape Abram

94   (Kola Inlet). *M. balthica* density at other Kola Inlet sites (Pala, Retinskoe and Nagornoe) was

95   much alike Western Murman sites (figures 2A and 3A). The Eastern Murman *M. balthica* mean

96   density was lower than in Western Murman and Kola Inlet and rarely exceeded 100 ind. m^{-2}

97   (Figure 3A). However, two major exceptions from general pattern were found in 2008

98   (1208 ± 73 ind. m^{-2} in Ivanovskaya bay and 387 ± 77 ind. m^{-2} in Yarnyshnaya bay respectively). In

99   Dalne-Zelenetskaya bay (Eastern Murman) mean long-term (from 2002 to 2008) abundance was

100   47 ± 3 ind. m^{-2} (Figure 2A).

101   The most common type of *M. balthica* size structure was bimodal, but both cases of prevalence

102   of larger and smaller molluscs could occur in same or subsequent year. So, in 2008 Yarnyshnaya

103   was dominated by 4 mm molluscs, while 17-18 mm-long *M. balthica* prevailed in nearby Dalne-

104   Zelenetskaya and Gavrilovo (Figure 4A).

105   Alive individuals of *C. edule* were revealed at 11 sites out of 18. We have not found any alive

106   cockles in Klimkovka, Dolgaya, Tyuva, Gavrilovo, Drozdovka, Ivanovskaya and Gremikha.

107   Density of *C. edule* in Pechenga, Retinskoe, Bolshaya Volokovaya was so low that there was no

108   possibility to estimate it using our sampling scheme, only solitary individuals were present at the

109   tidal flats during our observations. Only empty shells of *C. edule* were found in Gavrilovo and

110   Drozdovka*, while Shelpino population became extinct after 2009.

111   In Ura bay only solitary cockles were present in 2005, but in 2010 abundance increased up to

112   282 ± 68 ind. m^{-2}. The other site with rather high abundance was Pala bay (45 ± 9 ind. m^{-2} in 2006).

113   In subsequent 2007 cockle abundance at this site had dropped, and only solitary cockles were

114   present (Figure 2B). Cockle abundance was notably lower at all other sites (less than 10 ind. m^{-2}

115   at the majority of sites studied) (Figure 3B). Mean abundance at the Western Murman was

116   significantly higher than at other two regions (Kruskal-Wallis test: $\chi2 = 21.4$, $p < 0.001$).

117   Unimodal age structures in with prevalence of single *C. edule* generation were typical for most

118   sites (22-24 mm-long cockles in Ura bay, 2005; 26-28 mm in Shelpino, 2005 and 20-24 mm in

119   Pala, 2007) (Figure 4B).

120   DISCUSSION

121   Our results generally match with the expectation that the amphi-boreal species *Macoma*

122   *balthica* will show higher densities in the Barents Sea in comparison to the more temperate-zone

123   *Cerastoderma edule*. This cockle is supposed to be the most sensitive bivalve to low air

124   temperatures on European shores - severe winters were shown to cause mass mortalities among

125   adult *Cerastoderma edule* in the Wadden Sea (Strasser et al., 2001). What effects of severe

126   winters are more critical for cockle survival is still unclear, but probably the sudden rise of the

127   air temperature in subsequent spring may be even more crucial than winter freezing of upper

128   bottom layer during low tides (Strasser et al., 2001). The long-term monitoring data from the

129   Wadden Sea provided evidences that long-term variability in average winter temperatures affects

130   bivalve population dynamics in numerous ways (Beukema et al., 2009; Beukema & Dekker,

131 2014). Community-level analyses revealed that mild winters in the Wadden Sea give advantage

132 to recruitment in decapods *Crangon crangon* and *Carcinus maenas*, which in turn essentially

133 feed on postlarvae of bivalves *Macoma balthica*, *Cerastoderma edule*, *Mya arenaria* and *Mytilus*

134 *edulis* (Beukema & Dekker, 2014). The Barents Sea is lacking *Carcinus maenas.* The

135 distribution edge is in Northern Norway. *Crangon crangon* also cannot be regarded as an

136 important predator in the Barents Sea intertidal because it does not seem to form permanent

137 populations in the Murman Coast (Kuznetsov, 1960).

138 Regional variability in mean abundance, found in both *M. balthica* and *C. edule* could be

139 interpreted by a difference in general environmental conditions between Western and Eastern

140 Murman. West Murman is an area of numerous fjord-like bays, among which Kola Inlet is the

141 longest (57 km) and Pechenga and Ura bay are more typical – 16 and 19 km long respectively,

142 while Eastern Murman coast is relatively straight. Also, westerly Murman Coastal Current

143 dominates the nearshore hydrodynamics in Eastern Murman, while longer bays of Western

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

145 1995).

146 According to our data, mean *Macoma* abundance was significantly lower in Eastern Murman

147 sites in comparison to Western Murman and Kola Inlet sites. In 1973 mean density of

148 *M. balthica* at Dalne-Zelenetskaya bay (23 ± 9 ind. m^{-2}) was much alike the present-day values

149 (Agarova et al., 1976). At Western Murman and in Kola Inlet clam densities were comparable

150 with their densities in the White Sea, in the Baltic Sea and in the nearest waters – the northern

151 part of the Norwegian Sea (for example Semenova, 1974; Aschan, 1988; Bostrom & Bonsdorf,

152 2000; Oug, 2001; Varfolomeeva & Naumov, 2013; Rousi et al., 2013; Gerasimova &

153 Maximovich, 2013). Similar to the Eastern Murman values of mean *Macoma* abundances were

154 typical to the southern part of the Norwegian Sea and the Wadden Sea (Sneli, 1968; Beukema,

155 1976; Jensen & Jensen, 1985; Reise et al., 1994) (Figure 5A).

156 Populations of *Macoma balthica* in the South-Western Barents Sea (Murman coast) are

157 certainly not marginal within the species' European part of the range (figures 1A and 5A) –

158 *Macoma* also occurs in the Kara Sea on the North-East and quite typical for the White Sea

159 intertidal communities, where it reaches high densities (Semenova, 1974; Denisenko et al., 2003;

160 Strelkov et al., 2007; Gerasimova & Maximovich, 2013).

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

162 were dissimilar with other Eastern Murman localities, because in this site *Macoma* appeared to

163 be more subtidal than intertidal species – it occurs just below the low water level. Subtidal

164 *Macoma balthica* population was previously reported in the Pechora Sea (southeastern part of

165 the Barents Sea) with mean densities of 654 ind. m^{-2}, which is two times lower than in

166 Ivanovskaya (Denisenko et al., 2003).

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

168 not follow the "abundant centre" (Figure 5A) and is more like a "ramped north" (for names of

169 distribution shapes see Sagarin & Gaines, 2002). Surprisingly, mean individual densities of

170 bigger than spat-sized *Macoma* in Western Murman sites were more similar to those in the White

171 and Baltic Seas, and were higher than long-term mean values available for North Sea and Bay of

172 Biscay (see appendix A).

173 Mean densities of adult *Cerastoderma edule* on the Murman Coast of the Barents Sea, varying

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

175 presumably in the North Sea and Irish Sea (Beukema, 1989; Ivell, 1989; André & Rosenberg,

176 1991; Bachelet et al., 1992; Ramon, 2003; Dare et al., 2004) (Figure 5B). Long-term mean

177 density of cockles in the Dalne-Zelenetskaya bay was equal to previously reported values

178 (Agarova et al., 1976). Very similar densities to the Barents Sea cockle were previously reported

179 from Tromsø, North Norway (Oug, 2001). These data support the hypothesis that low abundance

180 is a typical feature of the northern part of the cockle range. Taking into account that at the

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

182 with long-term mean of 638 ind. m^{-2} (Gam et al., 2010) , abundance pattern could be probably

183   characterized as an "abundance center", but with a higher abundance at the southern range edge,

184   as compared to the Barents Sea.(Figure 5B). Current easternmost *Cerastoderma* local population

185   is located in Tryashina (~68° 59' N, ~36° 30' E), we did not find any alive cockles further east.

186   However, in Drozdovka (~100 km east from Tryashina) we have found two non-fossilized cockle

187   shells, which mean that temporary settlement of this species occurred here some years ago.

188   Murman coast clearly is a dynamic range edge for *Cerastoderma*, and thus in five other sites

189   (Pechenga, Retinskoe, Tyuva, Bolshaya Volokovaya, Gavrilovo) it was impossible to estimate

190   cockle density using standard sampling methods and only shells were found. No cockles were

191   also found in the inner part of the Kola Inlet, Cape Abram and Nagornoe (Figure 3B). We

192   suppose this could be explained by the known sensitivity of *Cerastoderma* to pollution load

193   (Savari et al., 1989), which should be significant near the city and port of Murmansk, largest

194   coastal industrial area in the Barents Sea region.

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

196   mass mortality events, when adult densities sharply decline from thousands of individuals to

197   single cockles per square meter due to a variety of factors. After that slow population recovery

198   takes place (Strasser at al., 2001; Malham et al., 2012; Callaway et al., 2013). In the Wadden Sea

199   during periods, called after Ducrotoy et al. (1991) as "recovery", cockle density may reach

200   54000 ind. m^{-2} including individuals of all age groups (Malham et al., 2012). According to our

201   study, the cockle population in Ura bay on Western Murman unambiguously had features of a

202   recovery phase in 2010 after "crisis" phase observed in 2005 (Figure 2B). During our first visit,

203   only solitary individuals were found across the tidal flat, while in 2010 mean cockle density was

204   282 ind. m^{-2}, which is the highest density value for the Barents Sea. Our results on cockle local

205   population recovery in Ura Bay support the dependence (at least partial) of Barents sea

206   populations of invertebrates and pelagic fish on larval drift from west (Gjøsaeter, 1995;

207   Mikkelsen & Pedersen, 2004).

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Table 1. Investigation sites and sampling details

| Region	Site (code)	Latitude, longitude	Observation years
Western Murman	Pechenga (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
	Severnoe Nagornoe (NG)	68.90, 33.06	2005
	Tyuva (TU)	69.17, 33.63	2005
	Bolshaya Volokovaya (BV)	69.27, 33.62	2005
Eastern Murman	Klimkovka (KL)	69.23, 34.64	2009
	Dolgaya (DO)	69.17, 33.63	2009
	Gavrilovo (GV)	69.17, 35.86	2008
	Yarnyshnaya (YA)	69.09, 36.05	2004 - 2008
	Dalne-Zelenetskaya (DZ)	69.11, 36.10	2002 - 2009
	Shelpino (SH)	69.10, 36.21	2005, 2008
	Porchnikha (PR)	69.08, 36.25	2006 - 2007
	Tryashina (TR)	68.99, 36.51	2008
	Drozdovka (DR)	68.30, 38.44	2008
	Ivanovskaya subtidal (IV)	68.29, 38.71	2008
	Gremikha (GR)	68.03, 39.85	2009
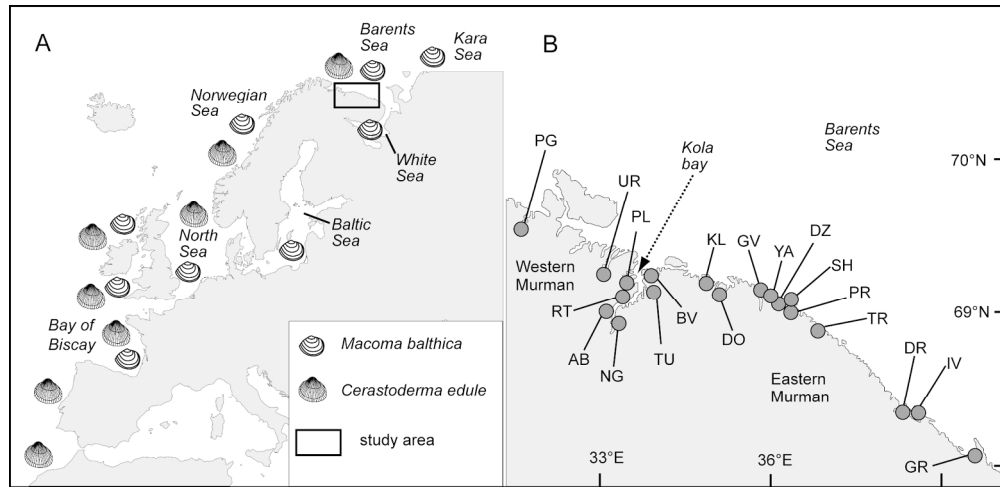
Fig. 1. Distribution range map of *Macoma balthica* (European part) and *Cerastoderma edule* (A) and study area map (B). See table 1 for sample sites details.
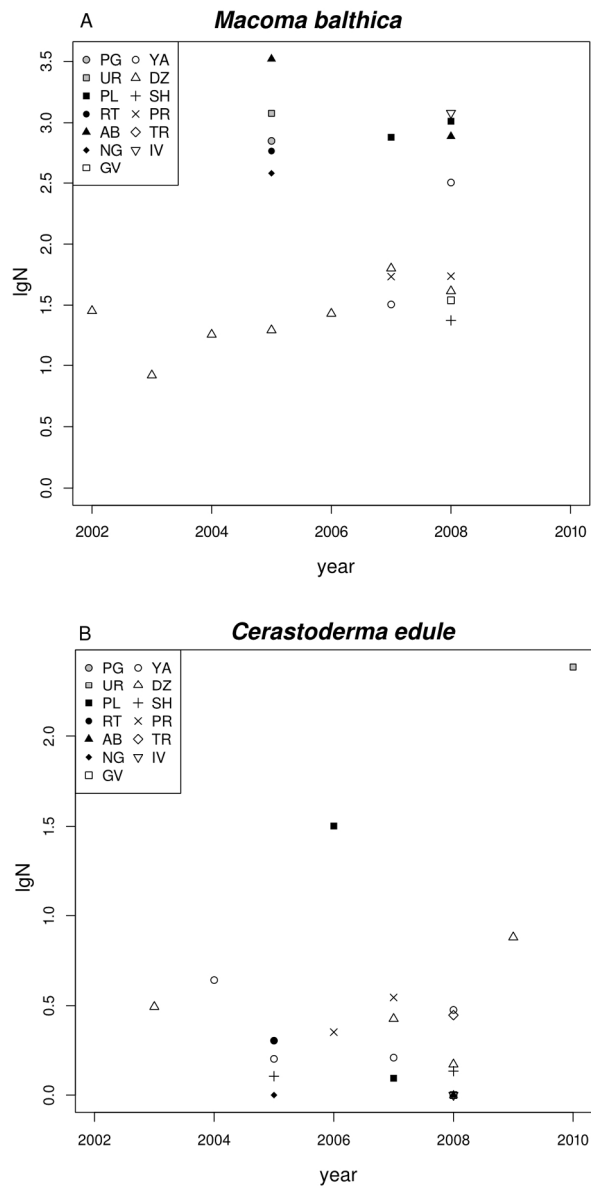175x85mm (300 x 300 DPI)

Fig. 2. Year-to-year variability of *Macoma balthica* (A) and *Cerastoderma edule* (B) mean abundance (lgN). Symbol colour corresponds to the region: Western Murman – solid grey, Kola Inlet – solid black and Eastern Murman – open symbols.
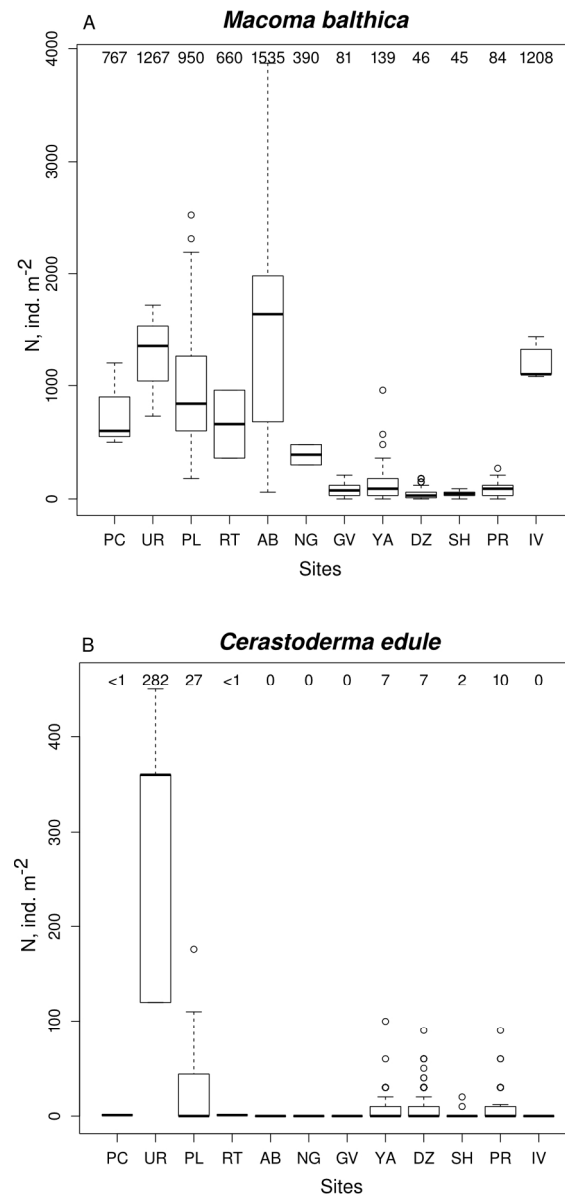101x208mm (300 x 300 DPI)

Fig. 3. 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.
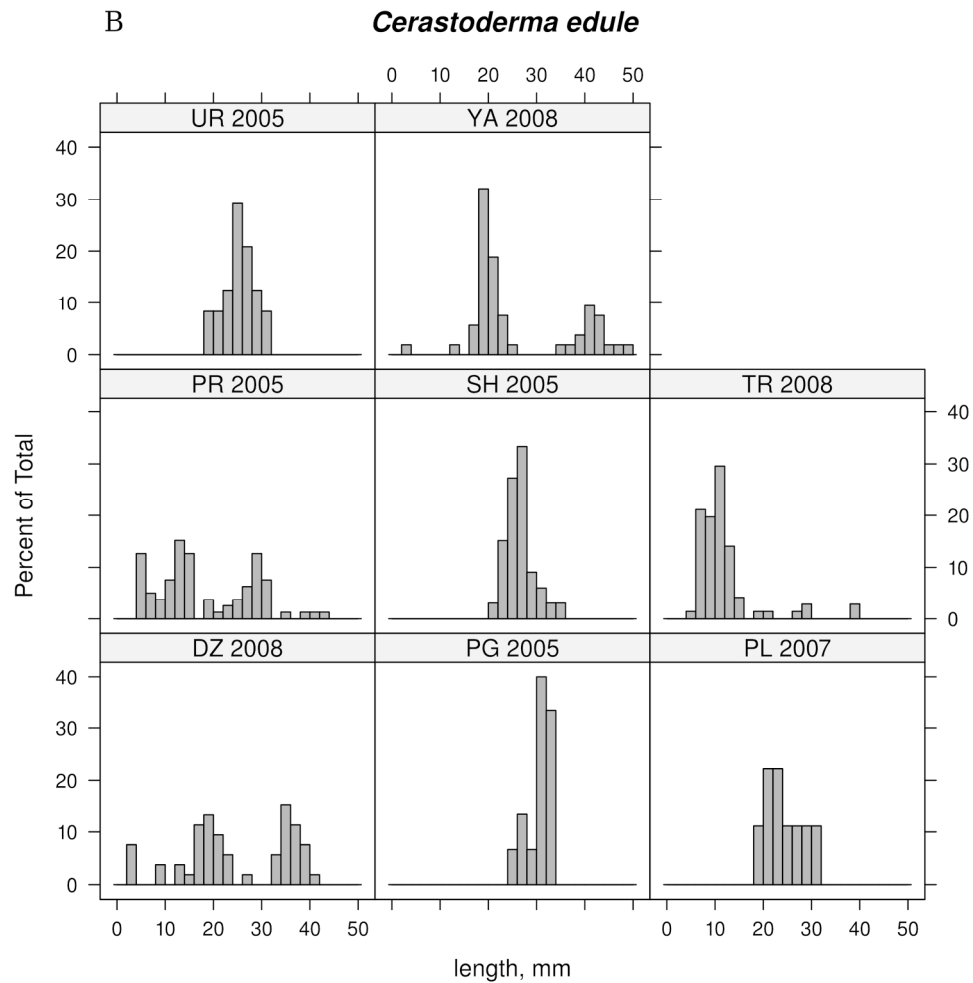101x210mm (300 x 300 DPI)
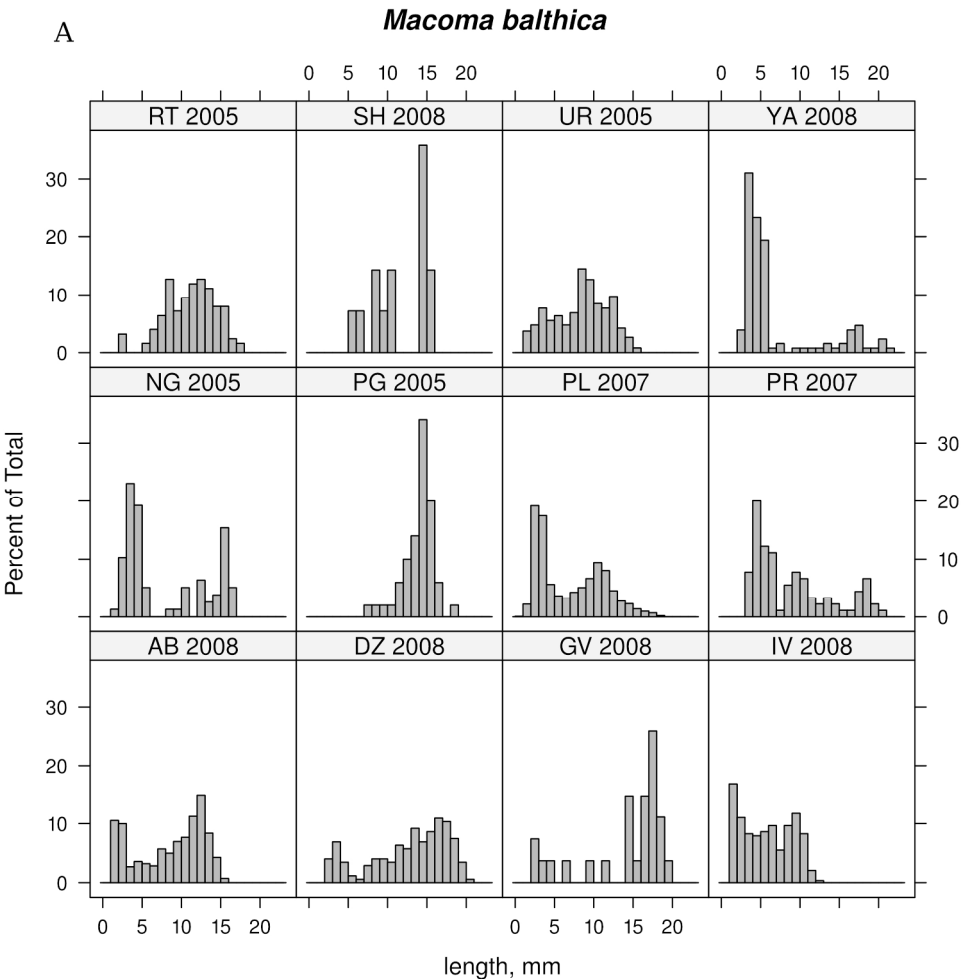
Fig. 4. Size frequency distributions of *Macoma balthica* (A) into 1 mm classes and *Cerastoderma edule* (B) into 2 mm classes.
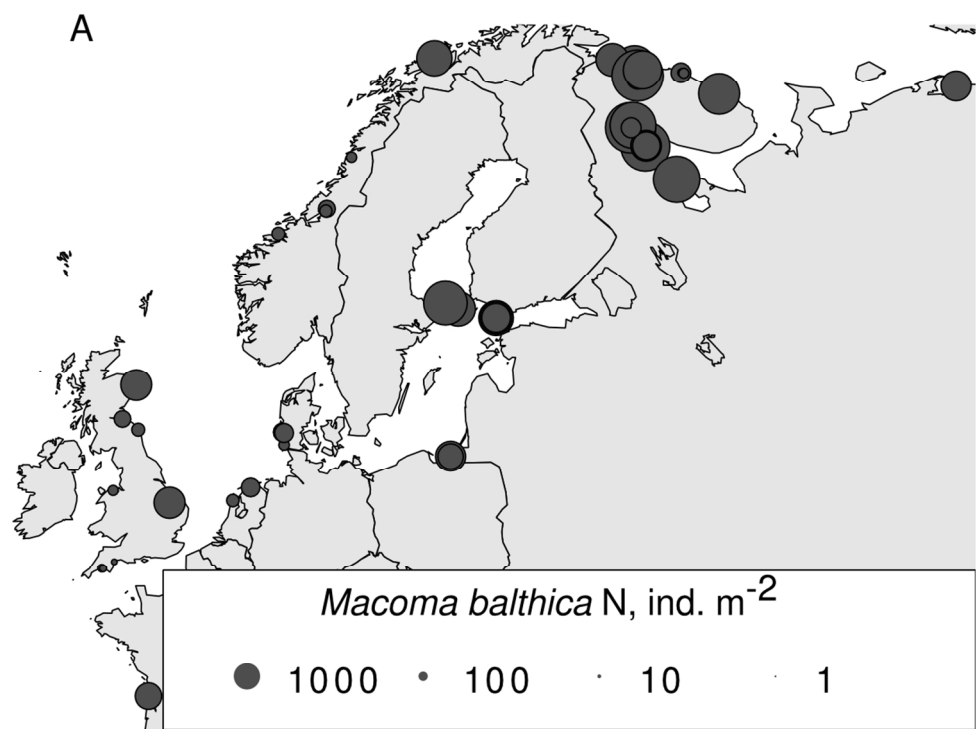211x211mm (300 x 300 DPI)

Fig. 4. Size frequency distributions of *Macoma balthica* (A) into 1 mm classes and *Cerastoderma edule* (B) into 2 mm classes.
211x211mm (300 x 300 DPI)

Fig. 5. Geographic abundance distributions of *Macoma balthica* (A) and *Cerastoderma edule* (B). ~~Circles squares are proportional to~~ mean abundance. For sources of data see Appendix A.
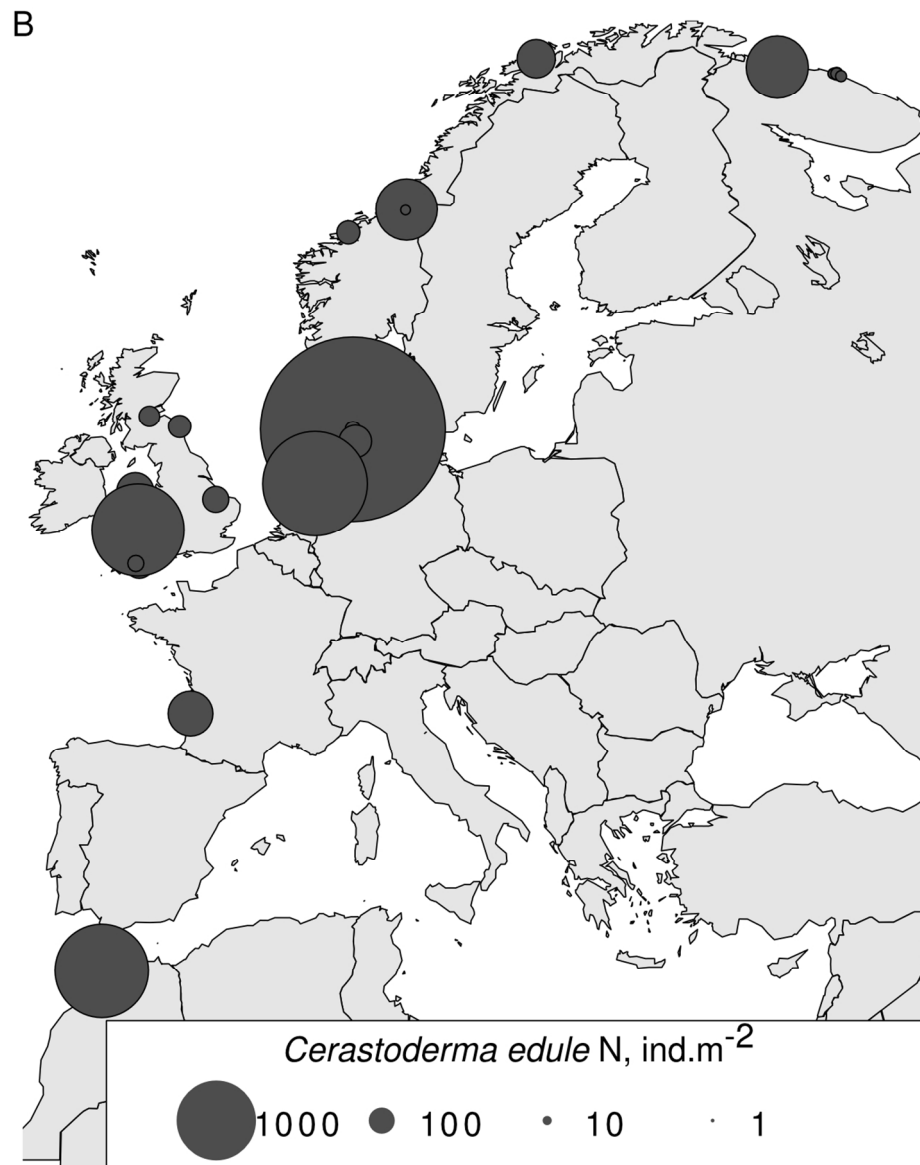109x84mm (300 x 300 DPI)

B

Fig. 5. Geographic abundance distributions of *Macoma balthica* (A) and *Cerastoderma edule* (B). Circles squares are proportional to mean abundance. For sources of data see Appendix A.
108x139mm (300 x 300 DPI)