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

Sophia Nazarova1,2,\*, Evgeny Genelt-Yanovsky1, Ksenia Shunkina3

1 – Department of Ichthyology and Hydrobiology, St Petersburg State University, 16 Line, 29, Vasilevsky Island, St Petersburg, 199178, Russia

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

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

\* Corresponding author: Sophia Nazarova, e-mail: [sophia.nazarova@gmail.com](mailto:sophia.nazarova@gmail.com)

*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. In both species, abundance was generally 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. 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, latitudinal variation

INTRODUCTION

Patterns of species' abundance at the biogeographic extremes, may provide insights into such essential issues in ecology as identification of borders between adjacent biogeographic regions and causes of species range limits. Large-scale distribution of species abundance is also a key element of applied sciences such as planning of protected areas and designation of species into regional Red Lists. A widespread paradigm, known as «abundant-centre hypothesis» (ACH) is widely used to test whether the highest species abundance belongs to the range centre and declines towards range edges (Sagarin et al., 2006). Intertidal fauna is an ideal test system for studying latitudinal gradients. In Western Europe, many intertidal and high subtidal marine invertebrates have extended ranges with distinct north (or north-eastern) and south (or south-western) limits characterized by diametrically opposed combination of environmental conditions. Recent studies on wide-spread marine coastal invertebrates have shown that abundance centre pattern does not apply to most species equally, and even closely related species could show different spatial patterns (Sagarin, Gaines, 2002; Rivadeneira et al., 2010).

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

Species ranges are not stable in time, often shifting, expanding and contracting (Gaston, 2009). Fluctuations of environmental variables, such as climate oscillations, may alter population fitness at the distribution limits and range shifts can lag behind environmental changes (Pfenninger 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 considered to be 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 of *Macoma balthica* and *Cerastoderma edule,* two key bivalve species at the tidal flats of the Barents Sea*. Macoma balthica* is currently regarded 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 (figure 1 A). Southern distribution range limit of *Macoma* has shifted several hundreds of kilometers north during last decades (Beukema et al., 2009). Pure *M. balthica balhica* northern 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). *Cerastoderma edule* range is shaped into at least two genetically different groups of populations along the North Atlantic coast, but separation between these groups does not have a subspecies level (Krakau et al., 2012). Earlier we suggested that low density of individuals is typical for *C.edule* in the Barents Sea, a North-Eastern distribution limit for the species (Genelt-Yanovskiy et al., 2010)(figure 1A).To study latitudinal clines in geographical abundance distributions, we put together published records of mean M.balthica and C.edule density across species' European ranges with our own observations from the Barents Sea.

MATERIALS AND METHODS

**Study area**

Murman Coast is a northern border of the Kola Peninsula with a coastal line of about 700 km, including numerous bays and fjords. The longest, Kola Bay, divide Murman Coast into two regions: Western Murman and Eastern Murman. Environmental conditions on Murman are determined by westerly warm Murman Coastal Current (Denisov & Dzhenyuk, 1995). Interaction between Murman Coastal Current and Arctic water backflow causes remarkable cooling gradient from West to East Murman. Owing to gradient changes in environment this whole area has transitional biogeographical status – from boreal to arctic zone (Zenkevich, 1963). 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 of Murman Coast.

**Sampling**

Samples were collected at 18 sites across the Murman coast (all for *C. edule* and 12 of them for *M. balthica)* (figure 1, table 1). The sampling took place in July–August, from 2002 to 2010. At sites inhabited by *Macoma* alone, 5 cm deep cores with a surface area 0.03 m-2 were taken; for sites where *Macoma* and *Cerastoderma* occurred together, 0.1 m-2 corers were used. All samples were sieved through 1 mm mesh. Each tidal level was characterized with five samples at all soft-bottom sites studied.

All collected bivalves were sorted, identified and counted. Shell length of each individual was measured using callipers to the nearest 0.5 mm. Age of individuals was determined by counting annual growth marks on outer side of the shell. This method of age estimation was used basing on previous studies of *Macoma* and *Cerastoderma* in the region, confirming that structural marks on shells of the molluscs in the subarctic seas reflect the annual growth patterns, due to the strong seasonal variation in sea water temperature (Agarova, 1979; Maximovich et al., 1992; Maximovich, Gerasimova, 2004, Nazarova et al, 2010).

**Statistical analysis**

Identical statistical procedures for both species were employed. We started with describing the abundances from each site. We used both medians and means as measures of central tendency and created Tukey boxplots (Tukey, 1976) to illustrate abundance variability. Data on abundance from individual samples from one site was used for plotting. Also year-to-year variability of mean abundance and size-frequency distributions of the species were analysed. Kruskal-Wallis test (Hollander, Wolfe, 1973) was used to compare regional average abundances. The data from published records of mean *C.edule* and *M.balthica* abundance are presented together with our own observations in two maps (figure 5). For the comparisons we used only mean densities of *Macoma* and *Cerastoderma* bigger than spat-sized individuals. Full details on all papers used in assessment of global distribution patterns are listed in electronic supplementary (appendix A).

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

RESULTS

The abundance of *M. balthica* at Western Murman and Kola Bay sites varied from hundreds to thousands individuals per square meter. *M. balthica* mean density was significantly different at three regions of the Murman coast (Kruskal-Wallis test: χ2 = 17.6, p < 0.0001). Highest mean *M.balthica* density (3350±520 ind. m-2) was observed in 2005 at Cape Abram (Kola Bay). *M.balthica* density at other Kola bay sites (Pala, Retinskoe and Nagornoe) was much alike Western Murman sites (figures 2A and 3A). The Eastern Murman *M. balthica* mean density was lower than in Western Murman and Kola bay and rarely exceeded 100 ind. m-2 (figure 3A). However, two major exceptions from general pattern were found in 2008 (1208±73 ind. m-2 in Ivanovskaya bay and 387±77 ind. m-2 in Yarnyshnaya bay respectively). In Dalne-Zelenestkaya bay (Eastern Murman), mean long-term (from 2002 to 2008) abundance was 47.4±2.83 ind. m-2 (figure 2A).

The most typical type of *M.balthica* size structure was bimodal, but both cases of prevalence of larger and smaller molluscs could occur in same or subsequent year. So, in 2008 Yarnyshnaya was dominated by 4 mm molluscs, while 17-18 mm-long *M.balthica* prevailed in nearby Dalne-Zelenetskaya and Gavrilovo (figure 4A).

Alive individuals of *C. edule* were revealed only at 11 sites out of 18. We have not found any alive cockles in Klimkovka, Dolgaya, Tyuva, Gavrilovo, Drozdovka, Ivanovskaya and Gremikha. Density of *C.edule* in Pechenga, Retinskoe, Bolshaya Volokovaya was so low that there was no possibility to estimate it using our sampling scheme, only solitary individuals were present at the tidal flats during our observations. Only empty shells of *C. edule* were wound in Gavrilovo and Drozdovka*,* while Shelpino population completely become extinct after 2009.

In Ura bay only solitary cockles were present in 2005, but in 2010 abundance increased up to 282±68 ind. m-2. The other site with rather high abundance was Pala bay (45±9 ind. m-2 in 2006). In subsequent 2007 cockle abundance at this site had dropped, and only solitary cockles were present (figure 2B). Cockle abundance was notably lower at all other sites (less then 10 ind. m-2 at most sites) (figure 3B). Mean abundance at the West Murman was significantly higher than at other two regions. (Kruskal-Wallis test: χ2 = 21.4, p < 0.001).

Unimodal age structures with prevalence of single *C.edule* generation was typical for most sites (22-24 mm-long cockles in Ura bay, 2005; 26-28 mm in Shelpino, 2005 and 20-24 mm in Pala, 2007) (figure 4B).

DISCUSSION

Our results generally match with the expectation that amphi-boreal species *Macoma balthica* will show higher densities in the Barents Sea in comparison to the more temperate-zone *Cerastoderma edule*. This cockle is supposed to be the most sensitive bivalve to low air temperatures on European shores – severe winters were shown to cause mass mortalities among adult *Cerastoderma edule* in theWadden Sea (Strasser et al., 2001). Which effects of severe winters are more critical for cockle survival is still unclear, but probably the sudden rise of the air temperature in subsequent spring may be even more crucial than winter freezing of upper bottom level during low tides (Strasser et al., 2001). Conversely, long-term monitoring data from the Wadden sea provided evidences that high winter temperatures negatively affects *Macoma* population dynamics in numerous ways and that . Community-level analyses revealed that mild warm winters in the Wadden sea give advantage to recruitment in decapods *Crangon crangon* and *Carcinus maenas*, which in turn essentially feed on postlarvae of bivalves *Macoma balthica*, *Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis* (Beukema, Dekker, 2014). Barents Sea is lacking *Carcinus maenas,* its north distribution edge belongs to North Norway. *Crangon crangon* also cannot be regarded as important predator on the Barents Sea intertidal because it does not seem to form permanent populations in the Murman coast (Kuznetsov, 1960).

ДАЛЬНИЙ ПЛЯЖ В 70хгг

Populations of *Macoma balthica* in the southwest Barents Sea (Murman coast) are certainly not marginal within the species' European part of the range – *Macoma* also occur in the Kara sea on the North-East and quite typical for the White Sea intertidal communities, where it reaches high densyities (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, westerly Murman Coastal Current 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 found even within West Murman and Kola Bay (figure 2A). Among all sites, the highest density was recorded in the inner part of the Kola Bay – in Cape Abram site (figure 2A). 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 (Olaffson, 1989). Despite we did not 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 (Olaffson, 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 subidal than intertidal species – it occurs just below the low water level. Subtidal *Macoma balthica* population was previously reported in the Pechora sea (SE part of the Barents sea) with mean densities of 654 ind. m-2, 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 3A) and is more likely a “ramped north” (for names of distribution shapes see Sagarin & Gaines, 2002). Surprisingly, mean densities of *Macoma* bigger than spat-sized 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).

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 5B). 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” (Gam et al., 2010).

Current easternmost *Cerastoderma* local population is located in Trashina bay (~68° 59’ N, ~36° 30’ E), we did not find any alive cockles further east. However, in Drozdovka bay (~100 km east from Trashina) we have found out two non-fossilized cockle shells, which mean 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, Tuyva, 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 2B). 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 at 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 2B). 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).

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**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.

**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 bay – solid black and Eastern Murman – open symbols.

**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.

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

**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.