Using an unprecedentedly large amount of material and a species distribution modeling approach (GAM Model 1 SDM), we demonstrated that such environmental predictors as surf level, distance to the port, status of the port (active vs abandoned), salinity at low tide, size of the nearest river, and substrate of fouling (fucoid algae vs bottom substrates) each influence the distribution of Mytilus edulis (ME) and M. trossulus (MT) in the White Sea at scales ranging from meters to tens of kilometers reflecting the partial divergence of their ecological niches.

Below we first discuss what species adaptations could stay behind revealed patterns of ME and MT segregation against different predictors. Then, the possible role of competition in segregation by substrates. Further, whether the same set of predictors can drive segregation outside the habitat we studied, the littoral fucoid belt, outside the White Sea and outside the Kola contact zone. Finally, we review the pros and cons of our approach to assessing ecological niche partitioning of sympatric species and make recommendations for further study of blue mussel species 'communities' and similar 'cryptic' taxa.

Ecological niche partitioning between MT and ME in the Kola contact zone.

In the light of our findings, the most expected habitat for ME in the White Sea littoral is a bottom substrate in a location exposed to wind, with a “normal” for the White Sea surface salinity (about 24 ppt) and away from ports and big rivers, while for MT it is an algal substrate in an area protected from wind, with reduced salinity and close to ports and big rivers. Of these ecological differences between species in the White Sea, only those related to ports and substrates were previously known (VS 11, Katolikova et al. 2016).

Salinity. It is generally recognized that the Baltic mussel (MT) is adapted to extremely low salinity (REF +++), which is also confirmed by ecophysiological data (Knöbel et al. 2021). Comparative ecophysiological data on MT and ME outside the Baltic are scarce and contradictory (Gardner & Thompson 2001; Qiu et al., 2002) and, until the present study, it has not been possible to convincingly prove species segregation by salinity in non-Baltic contact zones, including the Kola one (Moreau et al. 2005; … Katolikova et al. 2016; Marchenko et al. 2023), however some behavioral and biochemical differences in response to low salinity stress were revealed between MT and ME from the White Sea (Sokolova et al., 2024). For the White Sea, this state of knowledge may be due to at least three reasons, of which the first two may explain the vague relationship in other contact zones as well. First, the presence of other important factors affecting species segregation and masking the role of salinity. Second, the relatively narrow range of salinity in mussel habitats, in comparison with the Baltic Sea. Third, the curvilinear dependance of the proportion of MT in mixed settlements (Ptros) on salinity, where Ptros increases not only at reduced salinity, but also at extremely high, for the White Sea, salinity (up to 30 ppt, Fig. 2). This nonlinearity which may have prevented the correlation from being detected, can be explained in two ways. On the one hand, summer surface salinity above 24 ppt in some parts Kandalaksha Bay, may be associated with irregular episodes of upwelling (Dale & Prego 2003), bringing more salted deep water masses. This may act as a nonspecific stress for littoral animals, which MT can tolerate better (Katolikova et al. 2016, see also below). On the other hand, as detailed studies in the Barents Sea have shown (Khaitov et al. 2021, Marchenko et al. 2023), the method we used to predict Ptros from morphotype frequencies may slightly overestimate Ptros at salinities close to 30 ppt. Therefore, at this point we cannot rule out that the increased Ptros in sites with extremely high salinity is not an artifact of the method used for assessment of taxonomic structure.

Ports. According to the hypothesis of Vainola & Strelkov (2011), the confinement of MT to harbors in the White and Barents Seas reflects the history of its invasion into the region - by sea transport from the western Atlantic in the 20th century, which agrees with all genetic data (Simon, Wenne, Laakkonen ...). Katolikova et al. 2016 suggested that MT may also be more resistant to anthropogenic pollution and generally be a more opportunistic species, better adapted to disturbed habitats. (These characteristics are usually observed in successful invasive species (REF), which in the region is certainly MT).  Our observation that MT frequency is lower near abandoned ports than near active ones is consistent with this hypothesis. However, it should be kept in mind that unlike active ports, abandoned harbors may have been more isolated from the propagule pressure of MT in recent decades, which may have affected the size of populations of this species.

Surf. The confinement of ME and MT to locations with different surf levels among other things may be related to their known differences in the mechanical properties of shells and an ability to form dense aggregations. ME has a thicker, heavier and less flexible shell (Beaumont et al. 2008, Michalek et al, 2020 REF), and is more inclined to form tight clumps (REF) than MT. These features of ME may be adaptive on the exposed coasts. Unfortunately, there is no comparative data on species differences in byssus secretion and attachment strength, which also may influence their distribution by surf level, as well as across substrates.

Substrate. The same differences in shell structure and in aggregation behavior that may explain the segregation of species by surf may also explain their segregation by substrate. An ability to form dense aggregations is an adaptation to live on the bottom, not on the algae. Other things being equal, MT are lighter than ME due to thinner shells (Michalek et al, 2020), which may facilitate their life on algae. Further, fucoid thalluses may serve as shock absorbers for fragile MT (Katolikova 2016), as well as shelter them from starfish, which selectively prey on MT in mixed settlements (Khaitov et al. 2019, 2023).

Competition for substrate. Whatever physiological, morphological, behavioral, etc. features of MT and ME influence their segregation relative to different environmental factors ~~to the environmental factors~~ studied, interspecific competition may also be relevant. If there is interspecific competition, it is expected that the pattern of ecological segregation will be density dependent (+++). We tried to examine the role of mussel abundance in the degree of species segregation across substrates and found that while MT abundance had no significant effect, ME abundance, on the contrary, did: with increased abundance the degree of segregation increased (Fig. 4 B,C).

~~We interpret this pattern as a consequence of divergence of realized species niches, with ME displacing MT to algal thallomes that appear to be less suitable substrate for ME (see above).~~

Мысли

Thus, a useful definition of a species niche space is that it consists

of four major axes: resources, natural enemies, space and time.

Про мидий мы знаем мало про эти оси

Построение SDM для двух близких видов, сосуществующих в симптарии следует сразу орентировтаь на применение подходов JSDM.

If one assumes that local competitive dynamics occur on a faster time scale than spatial dynamics, then a patch can be interpreted as a local community within which coexistence is impossible and the collection of patches, a metacommunity within which regional coexistence is possible

The phenomenon of segregation of settlements of ME and MT by substrates can be interpreted as segregation of their settlements in small spatial scale. This segregation correlates with settlement density, which is expected if competition is the basis of this segregation. We interpret this pattern as a consequence of divergence of realized species niches, with ME displacing MT to algal thallomes that appear to be less suitable substrate for ME (see above). In future, our results can be considered in the context of the segregation hypothesis (Paccala, Levin, 1997), which theoreticlly predicts intra-specific clustering and inter-specific segregation, reflecting a trade-off between intraspecific and interspecific competition (Amarasekare, 2003). This hypothesis has been empirically supported in terrestrial ecology (Raventos et al., 2010) and the system of two similar (cryptic) mussel species coexisting in sympatry that we have studied may become a convenient model for testing this hypothesis in marine realm as well.

Pacala, S. W., & Levin, S. A. (1997). Biologically generated spatial pattern and the coexistence of competing species. *Spatial ecology: the role of space in population dynamics and interspecific interactions*, 204-232.

The predictive power of the SDM Model 1. Since the performance of our model  to classify sites into ME- and MT- dominated ones in an independent testing dataset from the White Sea was high (AUC = 0.8+), we trust that predictors included in the model explains most of variation in species distribution within the studied habitat - the littoral fucoid belt. In addition, the model also performed satisfactorily with independent data from Tyuva inlet in the Barents Sea (AUC ≈ 0.7), including sublittoral data, emphasizing the versatility of this set of predictors as regulators of the distribution of ME and MT in the Kola contact zone in general.

 We attribute the worst predictive value of our model for the Barents Sea data primarily to the following reasons. First, because of the large depth range of the sampling sites. It is known that ME and MT  in Tyuva are not randomly distributed by depth (REF). Second, because of the coarser categorization of samples into algal and bottom ones. Since fouling substrate was not taken into account during sampling (REF ++++), we had to predict it based on the projective cover of algae at the sampling site. Thirdly, we still do not know whether species are non randomly distributed across bottom and algal substrates in the sublittoral, where fucoids are replaced by kelps. Finally, the fact that our model more frequently overestimated Ptros in the Barents Sea data (false positive predictions) is consistent with the observation that the proportion of MT was declining in the studied area in the 2010s amidst seemingly stable environmental conditions in terms of predictors included in our SDM ~~(REF)~~. The latter  suggests the presence of additional, as yet unassessed factors regulating taxonomic structure.

Ecological niche partitioning between MT and ME in the Kola contact zone vs other zones.

Blue mussels represent a challenging model for studying the ecological niche partitioning between “cryptic” species in sympatry due to their wide distribution, biogeographic history and hybridization. ME and MT seemingly play similar ecological roles in their native oceans, Atlantic and Pacific respectively (REF) and therefore may inherently have strongly overlapping fundamental ecological niches. A set of contact zones between species in the Atlantics can be seen as different ecological (and evolutionary) experiments, set in very different environments (from Baltic to Spitzbergen), at different times (from the late post-glacial to the historical period, REF) and possibly with different “design” in the sense that in some zones one species may have been the original settler and in others another. In addition, competition (“character displacement”, REF), hybridization (“reinforcement of prezygotic reproductive isolation”, REF) and introgression (“transfer of adaptations”, etc. REF) could influence the divergence of their ecological phenotypes individualistically in different zones. All this suggests that zones should differ, and this hypothesis has been a leitmotif of some genetic research (RC, Vainola, Strelkov 2011, Bierne et al. 2011, Fraisse et al. … ).  We, however, believe that differences between species are most fundamental, and thus conspecific ecological phenotypes (“niches”) in different zones should be similar producing comparable patterns in species distributions.  Indeed, some results of our study support this assumption.

The observation that MT frequency is elevated in low salinity habitats not only in the Baltic Sea but also in the White Sea seems to resolve the old intrigue about seemingly contrasting salinity adaptations of the Baltic and all other Atlantic MT populations (e.g. RC 05, Katolikova, VS11, see also above). Further, increased MT frequency has been repeatedly observed in ~~calm~~ surf protected and freshened waters, such as in the tops of fjords around Bergen in Norway (Ridgway, Nævdal 2004) and Uummannaq in Greenland (Wenne et al. 2016), as well as in Loch Etive in Scotland (Beaumont et al. 2008), which is hardly a coincidence.

With the exception of the Baltic contact zone and salinity (as a main gradient of segregation), no non-random relationship between species distribution and any of the predictors significant in the White Sea has yet been convincingly demonstrated in the other contact zones. Data on the influence of surf are inconsistent (compare Bates, Innes 1995, Comesaña et al., 1999; Tam and Scrosati, 2013 and this study~~- все источники говорят что МТ любит прибой, а кто против?~~). Data on the role fouling substrates are, as far as we know, completely absent for other contact zones. If our ~~the~~ assumption is correct that the different preferences of ME and MT for sites with different surf and for different substrates is related to species differences in morphology and behavior (see above), then this should be manifested universally.

The intrigue about the increased resilience of MT to stress, particularly anthropogenic pollution, as in ports, also remains open. While toxicologic studies indicate that MT accumulates more heavy metals than ME (), increased incidence of MT has been repeatedly reported at polluted sites (Lobel et al. 1990; Brooks et al. 2015).

Obviously, 20 years after the classical review of RC 05 on the divergence of ecological niches of ME and MT in different contact zones, the time has come for a new such survey, and our experience with the Kola zone study may be useful here.

Desirable study design

The limitations associated with the approaches we used and ways to overcome them can be summarized as follows.

We used a “morphotype test” - rapid methodology for assessment of taxonomic structure of mussel settlements without genotyping that works well in habitats with salinity below 25 ppt in the Kola contact zone (Khaitov et al. 2021) but does not allow for direct assessment of species abundances, and the distinction of hybrids as a separate category. The latter partly excuses the fact that hybrids are relatively scarce in the Kola zone, but in some other zones this is not the case (Väinölä, Strelkov 2011; Wenne et al. 2020) and hybrids may be an important ecological actors in blue mussels ecology (Schwartz et al. 2024). Multilocus genotyping remains the best alternative to the “morphotype test”.

Although ME and MT differ universally in morphotype frequencies, the magnitude of the differences differs in different contact zones, as well as in locations with different salinities in the Arctic (). Consequently, if the “morphotype test” to be used there, it must be additionally calibrated (see Khaitov et all 2021 for recommendations).

Of course, we did not account for all potential predictors affecting species segregation (e.g., depth, Marchenko et al. 2023 or predators, Khaitov et al. 2019), and some of our predictors could have been estimated more carefully (for example, salinity at high water would be more informative for littoral mussels than at low water). However, since most of our predictors turned out to be significant, they should not be ignored going forward.

Our results allow us to be optimistic about the possibility of building reliable models that would allow us to predict where and under what conditions we can expect the formation of aggregations of a particular cryptic mussel species in the zone of their contact. For the most productive movement in this direction when investigating other contact zones, we find it necessary to adopt the following set of attitudes. First, a mixed mussel settlement should be considered as community of interacting species rather than as the sum of two populations, albeit linked by gene flow. The most appropriate way to do this would be to use technologies developed within the JSDM framework (see Ovaskainen, Abreg, 2020). Second, other species that are commonly ignored in genetic studies of mussel’s conact zones (starfish, fucoids, birds etc.) should also be included when studying this community. Third, no single, leading factor regulating mussel species segregation should be sought. All factors available for estimation should be included in the statistical model, the effects of which may become apparent only if other covariates are included in the SDM. Fourth, one should be careful about the shape of the relationships, which may be curvilinear (see Austin, 2002). GAM seems to be a good modelling tool but comparison with other techniques should be done (see Elith et al., 2006 as a good example from terrestrial ecology). And the last, most importantly, the design of the material collection should be spatially oriented, i.e., it should include the possibility to identify the role of factors acting at different spatial scales.