

## Reproductive isolation at contact zones

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## **ABSTRACT**

Speciation is among the most important evolutionary processes that contribute to biodiversity. It involves the formation of new species that have become reproductively isolated through a process that is not linear and varies in time and space. For divergent populations that still exchange genes, questions remain on how selective forces and demographic history can influence the maintenance and/or accumulation of multiple barriers to gene flow. In this thesis, I tackle these questions using contact zones between genetically-differentiated populations.

The salinity gradient between the marine North Sea and the brackish Baltic Sea impacts heavily on the adaptation of marine species living in this area. Our review found 23 out of 24 marine species with genetic data have formed divergent populations over this gradient. Population differentiation is strongly driven by divergent selection and/or temporal or spatial segregation, and it seems to be facilitated by ancestral variation. Another excellent example of divergent populations that show barriers to gene flow across contact zones is the intertidal snail *Littorina saxatilis*. This species is abundantly distributed on the European and North American Atlantic coasts and it is known for the Crab and Wave ecotypes, the first adapted to crab predation and the second adapted to wave exposure. In L. saxatilis, patterns of divergence have been analyzed using single nucleotide polymorphisms (SNPs), the most common source of genetic variation. Polymorphic short insertions and deletions (INDELs) are the second most abundant variant type but they have been overlooked in speciation studies. My analyses suggest that INDELs are more affected by purifying selection than SNPs. However, they also show patterns of divergent selection and thus, have potential as genetic markers for studies of adaptation and population divergence.

In *L. saxatilis*, shell size is an adaptive trait that is also important for mating. I found that the probability of mating is size-dependent (assortative mating) and there is sexual selection for small male size. Given the different local optima of shell size, this mating pattern contributes to reproductive isolation between ecotypes and simulations showed that gene flow was more reduced by sexual selection than by assortative mating. Barriers to gene flow may also occur during mating and determining when mating is successful requires knowing when sperm transfer starts. I found evidence suggesting that sperm transfer begins within a few minutes in *L. saxatilis* and seems largely independent of mating duration.

Reproductive isolation at contact zones may be strongly affected by divergent ecological selection and the species history, and without a large hybrid disadvantage, sexual selection may be a more important barrier than assortment. Whether these barrier effects will lead to complete reproductive isolation remains an open question.

Keywords: hybrid zone | gene flow | genetic variants | mating | local adaptation | marine species | speciation