

NEWS AND VIEWS PERSPECTIVE

Hybridization in postglacial marine habitats

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Abstract

Within the last few million years, repeated invasions from the North Pacific have brought evolutionarily divergent lineages of *Macoma balthica* clams into contact in the marginal and inland seas of northern Europe (Strelkov *et al.* 2007). These divergent *M. balthica* lineages now co-occur and hybridize extensively, blurring the distinction between the lineages and with some populations best described as ‘hybrid swarms’. This scenario matches the prediction that hybridization between distinct genetic entities can generate evolutionary novelty, particularly in new environments where hybrid fitness is equal to or exceeds parental types (Arnold 1997; Seehausen 2004).

Macoma balthica clams are common members of soft-bottomed communities throughout Arctic, boreal, and temperate areas. *Macoma balthica*, like many other cold-temperate marine species, extended their original range out of the Pacific Ocean to colonize the Atlantic Ocean after the opening of the Bering Strait approximately 3.5 million years ago (Vermeij 1991). Since this original Pliocene range expansion, new endemic species and subspecies have formed via allopatry on the Atlantic coasts. Following the initial invasion and speciation, North Atlantic and Arctic regions have been colonized again by *M. balthica* from the Pacific. Many of the colonized areas are habitats uncovered by Holocene deglaciation. This complex colonization history and resultant gene exchange among worldwide *M. balthica* populations is slowly being untangled, with important implications for understanding how species colonize and adapt to new habitats.

In this issue of *Molecular Ecology*, Strelkov *et al.* (2007) examine the genetic origins of *M. balthica* populations ranging from Scandinavia to the northern Arctic coast of Russia, areas that would have been under ice at the last glacial maximum. Surprisingly, many of these populations are not a single subspecies of *Macoma balthica*, but rather admixed aggre-

gates of both endemic European (*Macoma balthica rubra*) and newly arrived Pacific (*Macoma balthica balthica*) evolutionary lineages. These populations contain allozyme alleles typical of allopatric *M. b. rubra* and *M. b. balthica* populations, and in some instances, mtDNA haplotypes from both subspecies.

As described by Strelkov *et al.* (2007), hybridization between *M. b. rubra* and *M. b. balthica* in northern Europe has some unusual characteristics. In contrast to many other hybrid zones, there appear to be few impediments to gene flow between lineages. Within hybrid *Macoma* populations, there is extensive gene introgression and no significant linkage disequilibria among loci in the hybrids. These attributes are characteristic of a hybrid swarm where random mating is not blocked by reproductive isolation between parental taxa. This results in a remarkable situation where the individuals that predominate are not the parental types, but those whose genomes are a complex mosaic of both parental taxa. Therefore, there is no sustained presence or contemporary input of parental genotypes to the populations (as in bimodal hybrid zones), even though *M. b. rubra* is abundant along most of the European coastline and *M. b. rubra* populations are interdigitated with hybrid populations. Furthermore, individuals within *Macoma* hybrid swarms contain unique amalgamations of the parental genotypes, so that individual clams have combinations of loci that cannot co-occur in either parental subspecies. These observations are consistent with a selective advantage for hybrid genotypes.

Another striking observation from the study of Strelkov *et al.* (2007) is that northern European *Macoma* populations run the gamut from resembling typical Atlantic *M. b. rubra* populations to Pacific *M. b. balthica* in genetic composition. Estimates of the founding proportion of Pacific *M. b. balthica* to hybrid populations range from 14% to 89%. Proportions of *M. b. balthica* alleles are not correlated with geographical distance along any linear/coastline axis; indeed, many geographically proximate populations (especially those in the White Sea) are highly differentiated from each other. These observations suggest that hybridization has created a wide range of novel genotypes as these lineages continue to mix.

Determining if and how hybrid *Macoma* populations maintain idiosyncratic proportions of *M. b. rubra*- and *M. b. balthica*-type alleles will be fertile grounds for future research. A number of factors may play a role. First, contemporary population structure among hybrid populations could result from differing colonization histories. In a companion paper, Nikula *et al.* (2007) show that some *M. b. balthica* mtDNA haplotypes from the White and Barents Seas are identical to Pacific *M. b. balthica* haplotypes, whereas Baltic Sea haplotypes have a fixed substitution difference with Pacific haplotypes and some endemic diversity. These mtDNA patterns may reflect independent contributions of *M. b. balthica* genetic material

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Fig. 1 Color polymorphism in *Macoma balthica*.

to local European *M. b. rubra* populations and could contribute to differences between populations. A second structuring factor could be local barriers to larval dispersal, including impeded dispersal across poor habitat and hydrographic barriers (see Strelkov *et al.* 2007 for specific examples). A final factor may be the possibility that local environmental conditions select for different combinations of genes and alleles as a consequence of differing environmental conditions.

It remains to be seen whether or not other coastal taxa in the White and Barents Seas share a similarly convoluted history with *Macoma*. However, there are striking parallels between *Macoma* and other taxa inhabiting the better-studied inland Baltic Sea. The clearest analogy is to mussels in the *Mytilus edulis* species group that also have a history involving Pacific to Atlantic colonizations and subsequent gene flow between evolutionarily divergent lineages. As with *M. b. rubra* and *M. b. balthica* in the Baltic Sea, the Atlantic endemic *M. edulis* forms a hybrid swarm with genetic remnants of a Pacific *Mytilus trossulus* lineage (e.g. Väinölä & Hvilson 1991; reviewed by Riginos & Cunningham 2005 and references therein). In fact, for many taxa (including fishes and algae), Baltic Sea populations are genetically differentiated from Atlantic and North Sea populations with admixture between populations occurring at the narrow mouth of the Baltic (reviewed by Johannesson & André 2006; Strelkov *et al.* 2007).

These distinct genetic characteristics of many Baltic taxa (and possibly White and Barents Sea populations) may reflect genomic remnants of previously circum-Arctic taxa (Johan-

nesson & André 2006; Strelkov *et al.* 2007). Such boreal taxa would have extended their ranges into new habitats exposed by retreating glaciers, while temperate European taxa, such as *M. b. rubra* and *M. edulis*, moved northwards and interbred with the Arctic forms. Such a scenario does not preclude secondary contact between temperate and boreal taxa preceding the current interglacial period. The only way to understand these complex histories is to use hemisphere-wide sampling, as exemplified by the recent *Macoma* studies (Nikula *et al.* 2007; Strelkov *et al.* 2007).

Recent evaluations of natural hybrid zones have highlighted the role that hybridization can play in creating 'evolutionary novelty', by mixing historically separated genomic elements (Arnold 1997). Novel environments should facilitate such adaptive hybridization, because new gene combinations could be at an advantage in new circumstances (Arnold 1997; Seehausen 2004). In the postglacial coastal habitats of northern Europe, hybridization between divergent forms appears to be a regional phenomenon. The recent studies of *Macoma* (Nikula *et al.* 2007; Strelkov *et al.* 2007) provide clear models for investigating biogeographical histories and gene flow between boreal marine taxa. Examination of additional species in these marginal and inland seas will provide great insight into colonization of new environments and whether hybridization facilitates adaptation.

References

- Arnold ML (1997) *Natural Hybridization and Evolution*. Oxford University Press, New York.
- Johannesson K, André C (2006) Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology*, **15**, 2013–2029.
- Nikula R, Strelkov P, Väinölä R (2007) Diversity and trans-Arctic invasion history of mitochondrial lineages in the north Atlantic *Macoma balthica* complex (Bivalvia: Tellinidae). *Evolution*, **61**–4, 928–941.
- Riginos C, Cunningham CW (2005) Local adaptation and species segregation in two mussel (*Mytilus edulis* × *Mytilus trossulus*) hybrid zones. *Molecular Ecology*, **14**, 381–400.
- Seehausen O (2004) Hybridization and adaptive radiation. *Trends in Ecology & Evolution*, **19**, 198–207.
- Strelkov P, Nikula R, Väinölä R (2007) *Macoma balthica* in the White and Barents Seas: properties of a widespread marine hybrid swarm (Mollusca: Bivalvia). *Molecular Ecology*, **16**, 4110–4127.
- Väinölä R, Hvilson M (1991) Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (Mytilidae: Mollusca). *Biological Journal of the Linnean Society*, **43**, 127–148.
- Vermeij GJ (1991) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, **17**, 281–307.