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Mytilus hybridisation and impact on aquaculture: A minireview

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Abstract

The three species in the blue mussel complex (*Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus*) show varying levels of hybridisation wherever they occur sympatrically. The spatial variation in hybridisation patterns is potentially governed by environmental conditions, larval dispersal and aquaculture practices. Commercial mussel cultivation has been shown to increase hybridisation through introduction of non-native species or spat transfer. There is evidence that mussel cultivation may promote commercially less desirable phenotypes (e.g. fragile shells), however, to what extent hybridisation impacts aquaculture is currently not clear. The aim of this review is to summarize the available information on *Mytilus* hybridisation patterns in Europe and their promotion through aquaculture practices in order to shed light on the overall implications for the aquaculture industry.

Keywords:

Blue mussel, Mussel culture, Introgression, Local adaptation, Genetic selection

1 Introduction

In the Northern Hemisphere, the blue mussel species-complex is composed of three closely related species: *Mytilus edulis* (Linnaeus, 1758), *Mytilus galloprovincialis* (Lamarck, 1819) and *Mytilus trossulus* (Gould, 1850), which readily hybridise wherever their geographical distributions overlap (Gosling, 1992) (Fig 1). The three sister species form a biogeographic replacement series with respect to temperature (Fly & Hilbish, 2013) and their distribution patterns and hybridisation have been intensively investigated (e.g. Coghlan & Gosling, 2007; Väinölä & Strelkov, 2011). *M. edulis* is a cold-temperate species widely distributed in European waters, from the Atlantic coast of Southern France to the White Sea, with its southern range often overlapping the range of *M. galloprovincialis* (Seed & Suchanek, 1992). *M. galloprovincialis* is a warm-temperate species found along the coasts of the Black Sea, the Mediterranean Sea as well as parts of the northwest Atlantic coast. This species has evolved from a Mediterranean population of *M. edulis* (Vermeij, 1991) with a genetic "split" into an Atlantic and Mediterranean subgroup at the Almeira-Oran oceanographic front (Quesada *et al.*, 1995). *M. trossulus* is widespread along North European coasts (Väinölä & Strelkov, 2011) as well as the Baltic Sea (Väinölä & Hvilsom, 1991). Originally native to the northeast Pacific coast (Seed, 1992), *M. trossulus* spread to the northwest Atlantic shortly after the last glacial maximum (18,000–21,000 ybp) (Rawson & Harper, 2009). Northwest and northeast Atlantic *M. trossulus* populations are closely related suggesting a common ancestor from the Pacific before the two populations split (Väinölä & Strelkov, 2011). Overall, mussels within the *Mytilus edulis* species-complex possess a high degree of phenotypic plasticity, preventing their unequivocal taxonomic discrimination using morphological characteristics; an issue being further complicated by hybridisation in areas of overlapping occurrence (Seed, 1992). However, they show differences in physiological responses to environmental conditions: e.g. effects of temperature and salinity on heart rate (Braby & Somero, 2006) and heat tolerance (Tomanek & Zuzow, 2010).

In addition to the ecological importance of mussels in intertidal and subtidal communities, *M. edulis* and *M. galloprovincialis* are commercially cultivated along most European coasts using both tidal (on-bottom and bouchot type) and subtidal (on-bottom, raft and longline) techniques (Smaal, 2002). They represent the only two cultivated mussel species in Europe with 282 k tonnes produced in 2013 worth one billion USD (FAO, 2015). The present review summarizes the current knowledge about *Mytilus spp.* hybridisation in Europe, drivers of hybridisation by shellfish aquaculture and addresses potential implications of hybridisation for the mussel cultivation industry.

2 Hybridisation patterns and larval dispersal

Hybridisation between species of the blue mussel complex occurs readily in locations where their distributions overlap (Gosling, 1992) and where non-native species have been introduced through shipping or aquaculture activities, e.g. spat transfer in France (Bierne *et al.,* 2003). The extent of hybridisation varies depending on factors such as spawning synchrony (Toro *et al*., 2002), environmental conditions and local adaptation (Riginos & Cunningham, 2005) and human activities (Väinölä & Strelkov, 2011), ranging from low to very high frequencies of hybrid offspring (e.g. Dias *et al*., 2009).

A pronounced hybrid zone of *M. edulis* x *M. trossulus* can be found in the Baltic Sea (Fig 1). Here, extensive introgressions of *M. edulis* alleles from the saline North Sea into *M. trossulus* populations adapted to the low saline Baltic Sea have been documented for multiple nuclear markers (Me 15/16, EFbis, M7 lysin and ITS) (Kijewski *et al.*, 2006, Stuckas *et al*., 2009). The same pattern has been observed for *M. edulis* F (female) mitochondrial DNA (mtDNA) resulting in the complete absence of *M. trossulus* F mtDNA in the eastern Baltic. Both the mtDNA introgressions as well as the pronounced salinity gradient from the North Sea to the Baltic are likely to drive this hybridisation pattern (Riginos & Cunningham, 2005).

M. edulis and *M. galloprovincialis* hybridise in the wild along the Atlantic coast of Europe producing patches of both pure and hybrid populations (Beaumont *et al.*, 2004). Instead of a single genetic gradient from *M. galloprovincialis* in the South to *M. edulis* in the North, a mosaic pattern of successive transitions with differing frequencies in allele introgressions can be found along the Westcoast of France (Bierne *et al.*, 2003) and Cornwall (Gilg & Hilbish, 2003), which may be driven by larval dispersal patterns. Co-occurrences of all three *Mytilus* taxa have been recorded in Scotland, although hybridisation with *M. trossulus* is geographically restricted (see Section 4 for details) and occurs in higher frequencies at mussel farms indicating that rope culturing increases hybridisation (Beaumont *et al*., 2008).

Indeed, rope culturing may enhance gamete mixing and increase gene flow between sympatric species, as mussels possess a pelagic larval stage offering the potential for large-scale geographic dispersal over distances of ≥ 30 km (Gilg & Hilbish, 2003). However, environmental conditions including current patterns, temperature and salinity can act as barriers to larval dispersal and settlement (Dobretsov & Miron, 2001) as can food availability. In addition, post-settlement selection for specific genotypes can occur as a result of competition or predation (Gardner & Skibinski, 1991). Commercial rope culturing means that benthic predation is largely excluded and surface area for settlement is high allowing altered competitive interactions between individuals relative to seabed populations. Given enough temporal and spatial sympatry between *Mytilus spp*., gene introgression may inevitably occur as a result of high levels of gamete mixing.

3 Aquaculture driven hybridisation

The aquaculture industry has often been responsible for, but also benefited from, alien species introductions, both intentionally and unintentionally, affecting the gene pool of native species (Cox, 2004). An emblematic example is the introduction of Pacific oysters (*Crassostrea gigas*) in Europe in the 1960s for culturing purposes (Shatkin, 1997) leading to *C. gigas* becoming the dominant oyster species in several European coastal areas (Troost, 2010). For the production of blue mussels, seed supply either relies on natural settlement of spat or their translocation from other shellfish farms (Śmietanka *et al.*, 2004), which can lead to gene flow between cultivated and wild populations further promoting hybridisation (Goulletquer & Le Moine, 2002).

Shellfish aquaculture can therefore alter the genetic structure in mussels interspecifically due to the introgressions and fixation of certain alleles (Daguin *et al.*, 2001) as well as intraspecifically (Bierne *et al.*, 2003). Bierne *et al.* (2003) analysed the genetic structure of the mosaic hybrid zone between *M. edulis* and *M. galloprovincialis* along the European Atlantic coast and proposed spat transfer from cultivated stocks in the Bay of Biscay to the Mont Saint-Michel bay area has resulted in extensive gene mixing between sites.

Similarly in the Northeast Pacific, shellfish aquaculture has been suggested as one of the main introduction pathways of the non-native *M. galloprovincialis*, contributing to their hybridisation with native *M. trossulus* (Wonham, 2004). However, similar increases in hybridisation can also be found in Europe. An example is represented by the observed presence of *M. galloprovincialis* and *M. trossulus* alleles in Dutch waters (Śmietanka *et al*., 2004) being introduced with mussels from the British Isles (Kijewski *et al.*, 2009).

4 Impacts of hybridisation on the mussel aquaculture sector

Even though the ecological implications of co-occurring species are well understood, less attention has been given to sympatric *Mytilus spp.* and how their hybridisation impacts mussel aquaculture.

The cultivation of *M. trossulus* compared to sibling species is less valuable from an economical perspective since they possess thinner and weaker shells, lower meat yields and grey coloured meat (Penney *et al.*, 2007; 2008). In Scotland, the native species *M. edulis* interbreeds with the non-native *M. galloprovincialis* (see section 1) being cultivated together successfully along the Scottish coast (Fig 2). However in 2004, pure species and hybrids of all three genotypes within the blue mussel complex were detected in Loch Etive, representing the first recorded occurrence of *M. trossulus* in UK waters (Beaumont *et al.*, 2008). Production in Loch Etive, the former mainstay of the Scottish mussel industry (Scott *et al.*, 2010), collapsed by over 50% due to the presence of fragile shelled *M. trossulus* being easily damaged during harvest and grading processes (Beaumont *et al*., 2008). As a result, *M. trossulus* is now listed as commercially damaging species in Scotland (Scottish Government, 2014). Interestingly, their geographical distributions are restricted to only few locations on the Scottish west coast and further occur in higher frequencies at farm sites compared to natural intertidal habitats (Dias *et al.*, 2009; see Fig 2). Considering that *M. trossulus* is mostly found close to the water surface associated with lower salinities (Beaumont *et al.*, 2008), they may occupy a different environmental niche compared to the other two *Mytilus* species and further open up the potential to spread wider as local rainfall patterns increase with unknown consequences for the local mussel industry.

In general, when sympatric species hybridise, they exchange genes supporting the maintenance of genetic variation and the spread of adaptive gene complexes (reviewed by Storfer, 1999). This gene flow can increase disease resistance within mixed species populations, being crucial from an evolutionary perspective but also of increasing relevance for the aquaculture industry. Hybridisation may in fact improve cultured species traits such as growth, survival rate and environmental tolerance. For example, hybrid offspring of cultured abalone are more resistant to disease and thermal stress than their homozygote parents, *Haliotis discus hannai* and *Haliotis gigantea* (Liang *et al.*, 2014). Also, intentional hybridisation between the native weathervane scallop *Patinopecten caurinus* and the introduced Japanese scallop *Pecten yessoensis* in British Columbia, Canada, produced fast growing ‘Pacific’ scallop hybrids with high resistance to diseases and mortality (Smith, 2006). In contrast, gene flow can also act as a constraint to local adaptation or oppose local selection, as for example shown by *M. edulis*’ polymorphism at the aminopeptidase I (lap) allele (Koehn *et al*., 1983). However, whether hybridisation reveals positive or negative implications for the hybrid offspring depends on the “fitness” component investigated (e.g. growth rate, viability, reproductive success, parasite resistance) as well as area studied. In the *M. edulis* x *M. galloprovincialis* hybrid zone in northwest Europe, *M. galloprovincialis* genotypes possess a fitness advantage over *M. edulis* genotypes; so does their hybrid offspring showing on average a fitness comparable to one parent (*M. galloprovincialis*) and superior to the other (*M. edulis*) (reviewed by Gardner 1994b). In addition, conspecific crosses within the *M. edulis* x *M. trossulus* hybrid zone in the Northwest Atlantic showed higher rates of fertilization and larval survival compared to heterospecific crosses (Miranda *et al.*, 2010). Variation in fitness results from endogenous post-zygotic selection (Bierne *et al.*, 2006), differences in the background (parental) genotype and/or the presence of environmental variability (i.e. stress) and heterozygosity-fitness relationship (Gardner, 1994a).

Ultimately, the genetic composition of mussel recruits governs their geographical distribution and ability to adapt to site-specific habitat conditions. These species-specific traits can be exploited in selective breeding programmes aiming for resilient and efficient mussel strains, as currently investigated for New Zealand's green lipped mussel *Perna canaliculus* (Ragg N., unpublished data), as well as to ensure a constant seed supply in regions facing shortages in spat fall, such as the Shetland Isles in Scotland (Association for Scottish Shellfish Growers, pers. Communication).

5 Conclusions

This review highlights the complexity of determining the overall impact of *Mytilus spp.* hybridisation on the aquaculture industry. We conclude that the effects of hybridisation are dependent on the species cultured, environmental conditions encountered and culturing technique applied. Negative implications for mussel aquaculture linked to hybridisation have been shown for Scotland, attributed to the presence of undesirable *Mytilus trossulus* affecting harvest yields and product quality. Indeed, movement of mussel ropes may promote 'genetic pollution' leading to gene swamping and the potential for erosion of genetic resources. The elimination of undesirable genotypes or selection of favourable ones in selective breeding programmes will further change species/allele frequencies and impact both cultured stocks and co-occurring wild populations. Further monitoring on the occurrences of *M. trossulus* alleles should investigate wider regions of the genome by utilizing next generation sequencing technology, identifying pathways of gene flow of non-desirable genotypes into the gene pool of farmed stocks.

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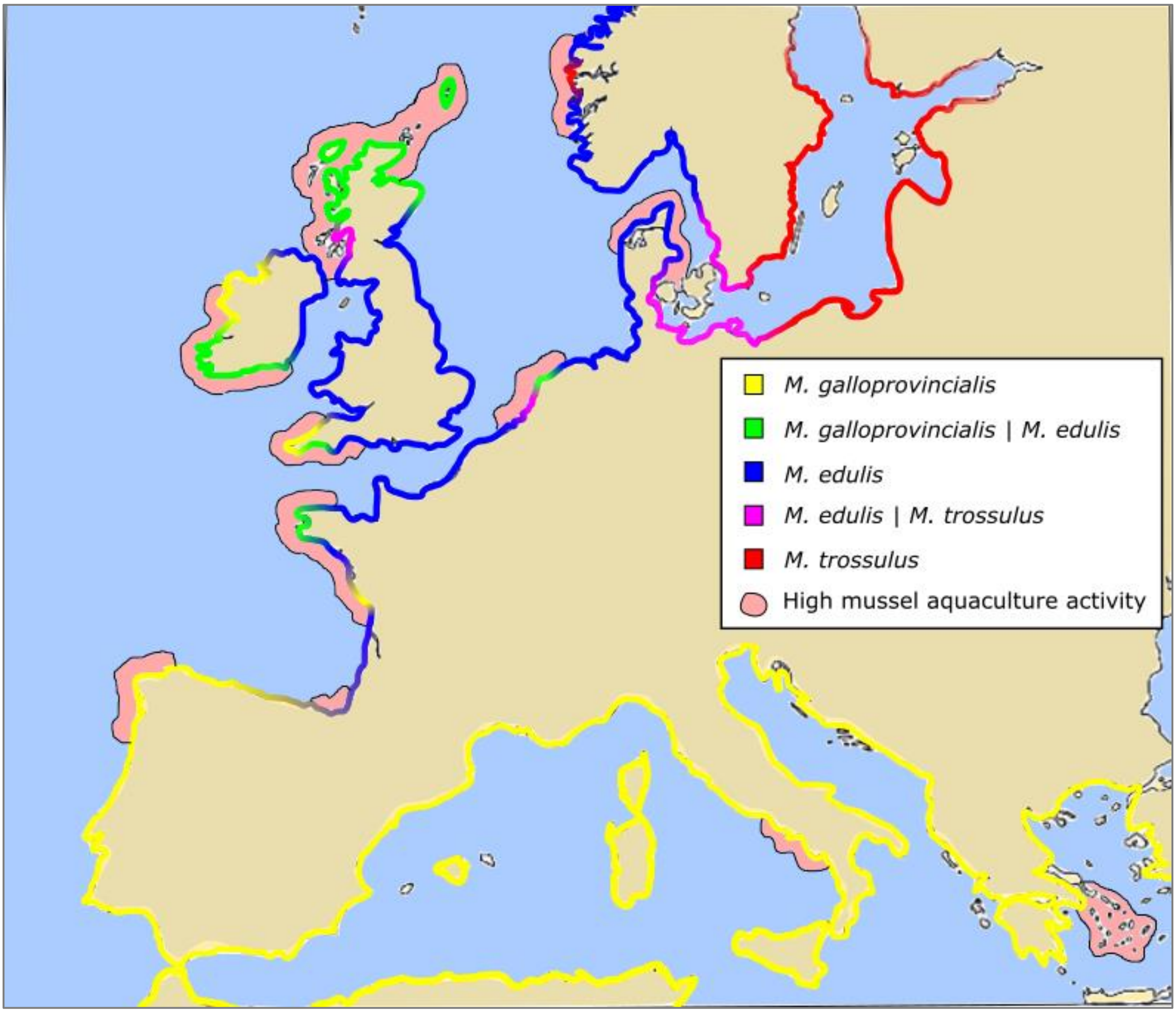

Fig. 1 Map of Europe showing the natural distribution of genotypes within the blue mussel species complex: *Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus*, and reported occurrences of their hybrids (see figure legend). Data is based on four nuclear markers (Bierne *et al.*, 2003; Daguin *et al.*, 2001; Kijewski *et al.*, 2009, 2011; Śmietanka *et a*l., 2004; Stuckas *et al.*, 2009). Coastal areas with high mussel aquaculture activity are highlighted (FAO, 2015).

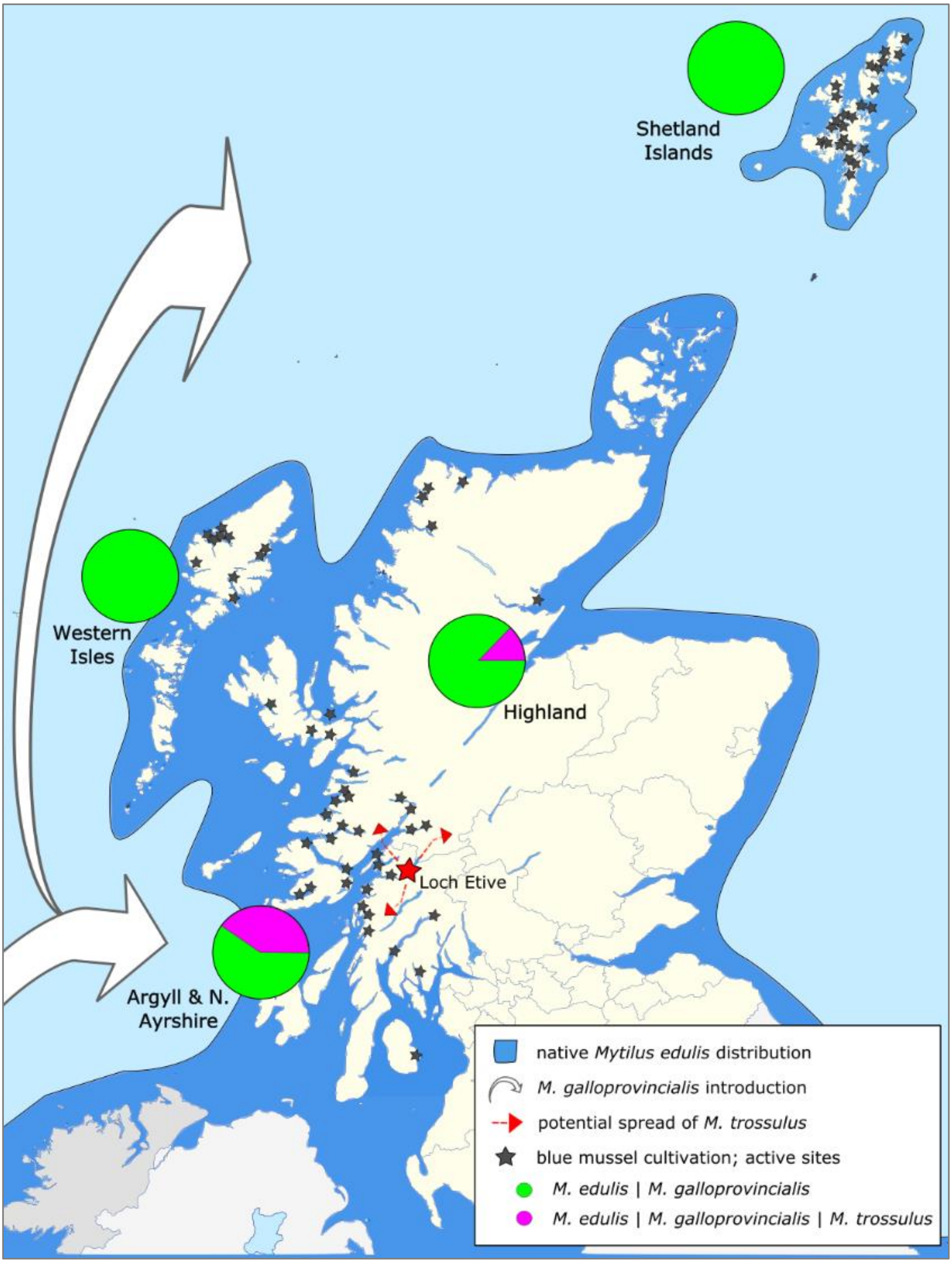

Fig. 2 Map of Scotland illustrating i) the natural distribution of the native species *Mytilus edulis*, ii) the introduction of the non-native *M. galloprovincialis* from a Mediterranean subgroup (Quesada *et al*., 1995), iii) active mussel aquaculture sites (Aquaculture Scotland, Oct. 2015) and detections of species-specific alleles at the Me15/16 locus at selected farm sites (Dias *et al*., 2009). Loch Etive is the only reported cultivation site with pure species of *M. trossulus*. Potential spreads of *M. trossulus* alleles under climate change predictions and enhanced aquaculture practises are indicated. See figure legend for symbols.