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***Mytilus* hybridisation and impact on aquaculture: A minireview**

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1 **Abstract**

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

12

13 **Keywords:**

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

15 1 Introduction

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

39 responses to environmental conditions: e.g. effects of temperature and salinity on heart
40 rate (Braby & Somero, 2006) and heat tolerance (Tomanek & Zuzow, 2010).

41

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

50

51 **2 Hybridisation patterns and larval dispersal**

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

59 A pronounced hybrid zone of *M. edulis* x *M. trossulus* can be found in the Baltic Sea (Fig 1).
60 Here, extensive introgressions of *M. edulis* alleles from the saline North Sea into *M.*
61 *trossulus* populations adapted to the low saline Baltic Sea have been documented for
62 multiple nuclear markers (Me 15/16, EFbis, M7 lysin and ITS) (Kijewski *et al.*, 2006, Stuckas

63 *et al.*, 2009). The same pattern has been observed for *M. edulis* F (female) mitochondrial
64 DNA (mtDNA) resulting in the complete absence of *M. trossulus* F mtDNA in the eastern
65 Baltic. Both the mtDNA introgressions as well as the pronounced salinity gradient from the
66 North Sea to the Baltic are likely to drive this hybridisation pattern (Riginos & Cunningham,
67 2005).

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

77

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

87 populations. Given enough temporal and spatial sympatry between *Mytilus spp.*, gene
88 introgression may inevitably occur as a result of high levels of gamete mixing.

89

90 **3 Aquaculture driven hybridisation**

91 The aquaculture industry has often been responsible for, but also benefited from, alien
92 species introductions, both intentionally and unintentionally, affecting the gene pool of
93 native species (Cox, 2004). An emblematic example is the introduction of Pacific oysters
94 (*Crassostrea gigas*) in Europe in the 1960s for culturing purposes (Shatkin, 1997) leading to
95 *C. gigas* becoming the dominant oyster species in several European coastal areas (Troost,
96 2010). For the production of blue mussels, seed supply either relies on natural settlement of
97 spat or their translocation from other shellfish farms (Śmietanka *et al.*, 2004), which can
98 lead to gene flow between cultivated and wild populations further promoting hybridisation
99 (Gouletquer & Le Moine, 2002).

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

106 Similarly in the Northeast Pacific, shellfish aquaculture has been suggested as one of the
107 main introduction pathways of the non-native *M. galloprovincialis*, contributing to their
108 hybridisation with native *M. trossulus* (Wonham, 2004). However, similar increases in
109 hybridisation can also be found in Europe. An example is represented by the observed

110 presence of *M. galloprovincialis* and *M. trossulus* alleles in Dutch waters (Śmietanka *et al.*,
111 2004) being introduced with mussels from the British Isles (Kijewski *et al.*, 2009).

112

113 **4 Impacts of hybridisation on the mussel aquaculture sector**

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

117 The cultivation of *M. trossulus* compared to sibling species is less valuable from an
118 economical perspective since they possess thinner and weaker shells, lower meat yields and
119 grey coloured meat (Penney *et al.*, 2007; 2008). In Scotland, the native species *M. edulis*
120 interbreeds with the non-native *M. galloprovincialis* (see section 1) being cultivated
121 together successfully along the Scottish coast (Fig 2). However in 2004, pure species and
122 hybrids of all three genotypes within the blue mussel complex were detected in Loch Etive,
123 representing the first recorded occurrence of *M. trossulus* in UK waters (Beaumont *et al.*,
124 2008). Production in Loch Etive, the former mainstay of the Scottish mussel industry (Scott
125 *et al.*, 2010), collapsed by over 50% due to the presence of fragile shelled *M. trossulus* being
126 easily damaged during harvest and grading processes (Beaumont *et al.*, 2008). As a result,
127 *M. trossulus* is now listed as commercially damaging species in Scotland (Scottish
128 Government, 2014). Interestingly, their geographical distributions are restricted to only few
129 locations on the Scottish west coast and further occur in higher frequencies at farm sites
130 compared to natural intertidal habitats (Dias *et al.*, 2009; see Fig 2). Considering that *M.*
131 *trossulus* is mostly found close to the water surface associated with lower salinities
132 (Beaumont *et al.*, 2008), they may occupy a different environmental niche compared to the

133 other two *Mytilus* species and further open up the potential to spread wider as local rainfall
134 patterns increase with unknown consequences for the local mussel industry.

135

136 In general, when sympatric species hybridise, they exchange genes supporting the
137 maintenance of genetic variation and the spread of adaptive gene complexes (reviewed by
138 Storfer, 1999). This gene flow can increase disease resistance within mixed species
139 populations, being crucial from an evolutionary perspective but also of increasing relevance
140 for the aquaculture industry. Hybridisation may in fact improve cultured species traits such
141 as growth, survival rate and environmental tolerance. For example, hybrid offspring of
142 cultured abalone are more resistant to disease and thermal stress than their homozygote
143 parents, *Haliotis discus hannai* and *Haliotis gigantea* (Liang *et al.*, 2014). Also, intentional
144 hybridisation between the native weathervane scallop *Patinopecten caurinus* and the
145 introduced Japanese scallop *Pecten yessoensis* in British Columbia, Canada, produced fast
146 growing 'Pacific' scallop hybrids with high resistance to diseases and mortality (Smith, 2006).

147 In contrast, gene flow can also act as a constraint to local adaptation or oppose local
148 selection, as for example shown by *M. edulis*' polymorphism at the aminopeptidase I (lap)
149 allele (Koehn *et al.*, 1983). However, whether hybridisation reveals positive or negative
150 implications for the hybrid offspring depends on the "fitness" component investigated (e.g.
151 growth rate, viability, reproductive success, parasite resistance) as well as area studied. In
152 the *M. edulis* x *M. galloprovincialis* hybrid zone in northwest Europe, *M. galloprovincialis*
153 genotypes possess a fitness advantage over *M. edulis* genotypes; so does their hybrid
154 offspring showing on average a fitness comparable to one parent (*M. galloprovincialis*) and
155 superior to the other (*M. edulis*) (reviewed by Gardner 1994b). In addition, conspecific
156 crosses within the *M. edulis* x *M. trossulus* hybrid zone in the Northwest Atlantic showed

157 higher rates of fertilization and larval survival compared to heterospecific crosses (Miranda
158 *et al.*, 2010). Variation in fitness results from endogenous post-zygotic selection (Bierne *et*
159 *al.*, 2006), differences in the background (parental) genotype and/or the presence of
160 environmental variability (i.e. stress) and heterozygosity-fitness relationship (Gardner,
161 1994a).

162
163 Ultimately, the genetic composition of mussel recruits governs their geographical
164 distribution and ability to adapt to site-specific habitat conditions. These species-specific
165 traits can be exploited in selective breeding programmes aiming for resilient and efficient
166 mussel strains, as currently investigated for New Zealand's green lipped mussel *Perna*
167 *canaliculus* (Ragg N., unpublished data), as well as to ensure a constant seed supply in
168 regions facing shortages in spat fall, such as the Shetland Isles in Scotland (Association for
169 Scottish Shellfish Growers, pers. Communication).

170

171 **5 Conclusions**

172 This review highlights the complexity of determining the overall impact of *Mytilus spp.*
173 hybridisation on the aquaculture industry. We conclude that the effects of hybridisation are
174 dependent on the species cultured, environmental conditions encountered and culturing
175 technique applied. Negative implications for mussel aquaculture linked to hybridisation
176 have been shown for Scotland, attributed to the presence of undesirable *Mytilus trossulus*
177 affecting harvest yields and product quality. Indeed, movement of mussel ropes may
178 promote 'genetic pollution' leading to gene swamping and the potential for erosion of
179 genetic resources. The elimination of undesirable genotypes or selection of favourable ones
180 in selective breeding programmes will further change species/allele frequencies and impact

181 both cultured stocks and co-occurring wild populations. Further monitoring on the
182 occurrences of *M. trossulus* alleles should investigate wider regions of the genome by
183 utilizing next generation sequencing technology, identifying pathways of gene flow of non-
184 desirable genotypes into the gene pool of farmed stocks.

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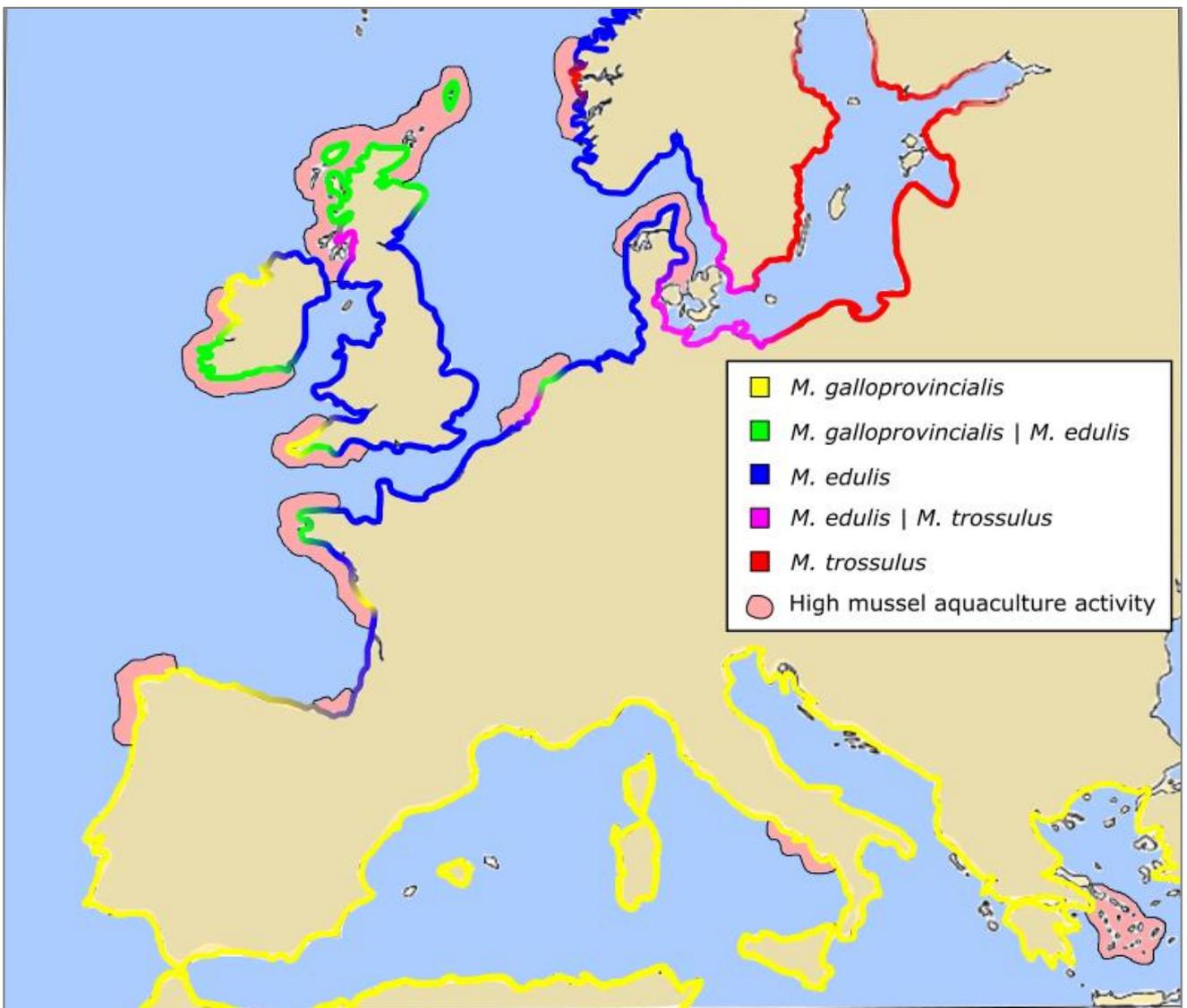


Fig. 1 Map of Europe showing the natural distribution of genotypes within the blue mussel species complex: *Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus*, and reported occurrences of their hybrids (see figure legend). Data is based on four nuclear markers (Bierne *et al.*, 2003;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

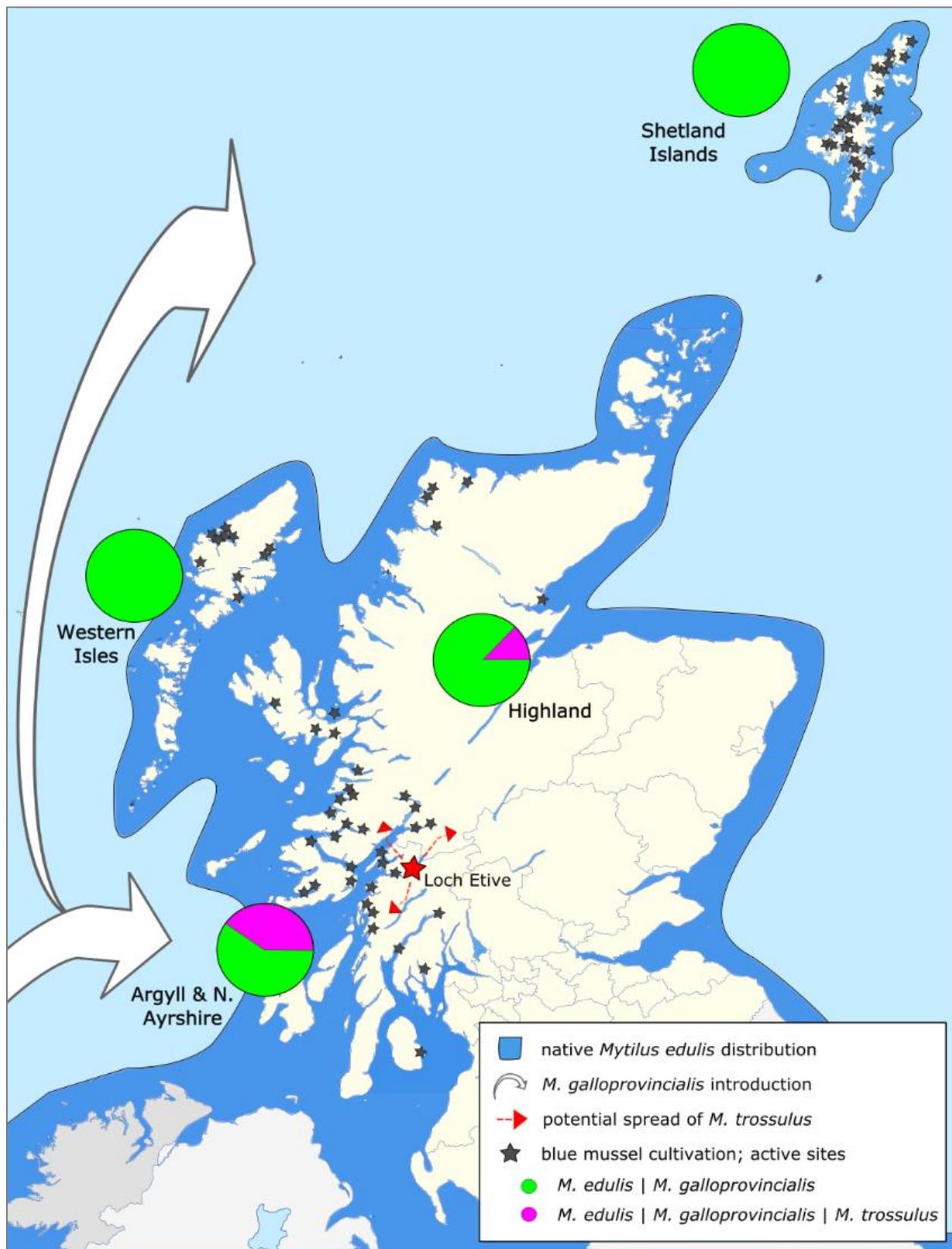


Fig. 2 Map of Scotland illustrating i) the natural distribution of the native species *Mytilus edulis*, ii) the introduction of the non-native *M. galloprovincialis* from a Mediterranean subgroup (Quesada *et al.*, 1995), iii) active mussel aquaculture sites (Aquaculture Scotland, Oct. 2015) and detections 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.