



Three species of *Mytilus* and their hybrids identified in a Scottish Loch: natives, relicts and invaders?

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ABSTRACT

Three species of the mussel, *Mytilus*, occur in the North Atlantic region, *M. edulis*, *M. galloprovincialis* and *M. trossulus*, and hybrid zones are present where their distributions overlap. *M. edulis* is a native species in the UK. *M. galloprovincialis* originated in the Mediterranean and its distribution extends northwards along the Atlantic seaboard to Scotland. Baltic Sea mussels have a *M. trossulus* ancestry but are highly introgressed by *M. edulis*. In recent decades, farming of mussels on long-line rope culture systems has been introduced into Scotland. On farms in Loch Etive, a form of mussel with a fragile shell and a different shape to either *M. edulis* or *M. galloprovincialis* has been increasing in frequency over recent years. Samples of fragile shelled, normal strong shelled and intermediate mussel types were sampled from two farms in 2006 and compared with samples of *M. edulis*, *M. galloprovincialis* and *M. trossulus* from other sources where their species identity is well established. Abundance relative to depth, shell strength, condition index and shell morphology were analysed together with 5 allozyme loci and one nuclear DNA genetic marker (Me 15/16). The fragile shelled mussels, and many of those classed as intermediate, were identified as a mixture of *M. trossulus* and *M. trossulus* × *M. edulis* hybrids. This identification was strongly supported by both morphological and genetic data and is the first record of the presence of *M. trossulus* in UK waters. *M. trossulus* in Loch Etive are most likely to be a post-glacial relict population restricted to the low salinity area of the Loch that has recently increased in abundance due to commercial mussel growing activity. In addition, individual mussels of all three species and their hybrids were detected amongst Loch Etive mussels. This is the first genetic demonstration of all three species and their hybrids occurring together in one location in the Atlantic region and provides a unique opportunity to study the processes of speciation, divergence, and introgression in the genus *Mytilus*.

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1. Introduction

The taxonomy of the common species of smooth shelled mussels in the genus *Mytilus* was uncertain before the advent of allozyme genetics (McDonald et al., 1991; Gosling, 1992) but there are now three recognised species of closely related mussels: *M. edulis* (Linnaeus, 1758), *M. galloprovincialis* (Lamarck, 1819) and *M. trossulus* (Gould, 1850). It is believed that *M. trossulus* originally evolved in the Pacific and first colonised the northern Atlantic when the Bering Strait opened 3.5 million years ago (Riginos and Cunningham, 2005). *M. edulis* then probably arose in the Atlantic by allopatric speciation (Vermeij, 1991). *M. galloprovincialis* is believed to have developed in the Mediterranean while it had restricted connection to the Atlantic (Riginos and Cunningham, 2005).

A second, more recent invasion of Pacific mussels into the Atlantic, during the Pleistocene or Holocene, has resulted in two *M. trossulus*-colonised regions, one in the Canadian Maritimes, and the other in the Baltic Sea (Riginos and Cunningham, 2005). Väinölä and Hvilson (1991) propose that *M. trossulus* may have been widely distributed in Europe and colonised the Baltic approximately 7500 years ago when there was an intrusion of North Sea water into the Baltic. *M. edulis* then gradually out-competed *M. trossulus* elsewhere in Europe. The Baltic Sea remained the last stronghold for *M. trossulus* because *M. edulis* could not withstand the very low salinities present but there has nevertheless been significant hybridisation and introgression and Baltic mussels have been labelled a “hybrid swarm” (Riginos and Cunningham, 2005). The existence of *M. galloprovincialis* and *M. edulis* in parts of the southern hemisphere is thought to be a result of transequatorial Atlantic migrations during the Pleistocene era (Hilbish et al., 2000).

At the present time *M. edulis* is probably the most abundant mussel in Europe and the north Atlantic but *M. galloprovincialis* has expanded out of the Mediterranean and now exists in a patchy mosaic of pure species and hybrids with *M. edulis* along the west coast of

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Europe from France in the south to the Shetlands in the north (Gosling, 1992). On the other hand, *M. trossulus* was thought to be restricted in Atlantic regions to the Baltic Sea and the Canadian Maritimes. However, this species might also be present in Norway (Ridgway and Naevdal, 2004) and the Netherlands (Šmeitanka et al., 2004). The hybrid zone between *M. trossulus* and *M. edulis* at the entrance to the Baltic Sea is narrow and distinct, while the hybrid zone in the Canadian Maritimes is much more extensive and has a less clearly defined mosaic pattern (Comesaña et al., 1999; Innes and Bates, 1999). Riginos and Cunningham (2005) have proposed that these two populations of *M. trossulus*, and their inter-relationship with *M. edulis*, differ mainly as a result of different environmental forces. The major determinant of distribution in the Baltic Sea is salinity with *M. trossulus* able to out-compete *M. edulis* at low salinities. However, in the Canadian Maritimes, wave exposure seems to favour *M. trossulus* leading to higher abundance of *M. edulis* in sheltered and often lower salinity, locations (Riginos and Cunningham, 2005). Indeed, Gardner and Thompson (2001) have shown experimentally that low salinities induced higher mortalities of *M. trossulus* than *M. edulis* in some Canadian populations.

Where the three *Mytilus* species are allopatric there are fairly distinct morphological differences between them that aid identification, but where their distributions overlap, hybridisation and introgression (e.g. Skibinski et al., 1983; Gardner, 1997; Hilbish et al., 2002) is a common occurrence and makes these morphological distinctions ineffective as diagnostic tools. In addition, all three mussel species can exhibit environmentally induced phenotypic plasticity such that position on the shore, degree of exposure, salinity and other factors can strongly influence shell shape and strength (Seed, 1968; Kautsky et al., 1990; Väinölä and Hvilson, 1991; Riginos and Cunningham, 2005).

Allozyme data provide more reliable identification of the three species, but no individual locus is completely diagnostic for any of the species (Gosling, 1992).

Allozyme genetic distances (Nei, 1978) between European populations of *M. edulis*, *M. trossulus* and *M. galloprovincialis* lie between 0.17–1.17 (Skibinski et al., 1980; Bulnheim and Gosling, 1988; Väinölä and Hvilson, 1991) which is in the range of sub-species to species (Ferguson, 1980). Although there is continuing uncertainty about the specific status of these three *Mytilus* taxa most authors refer to them as species for the sake of convenience (e.g. Gosling, 1992; Riginos and Cunningham, 2005).

Mitochondrial DNA in *Mytilus* is unusual in that it displays doubly uniparental inheritance (DUI). Distinctly different male and female mtDNA molecules are inherited with females having exclusively female mtDNA and males having both types with the male mtDNA concentrated in the gonadal tissue (Skibinski et al., 1994; Zouros et al., 1994; Breton et al., 2007). DUI is disrupted by hybridisation (Rawson et al., 1996a; Wood et al., 2003b; Kijewski et al., 2006) and this may play a role in maintaining hybrid zones. The complexity of mtDNA inheritance means that mtDNA markers have not generally been developed for the purposes of species identification (Šmeitanka et al., 2004).

Several nuclear DNA markers have been developed to assist discrimination and to study hybridisation in all three species of mussels (e.g. Heath et al., 1995 (ITS); Inoue et al., 1995 (Me15/16); Rawson et al., 1996b (Glu-5'); Rawson et al., 2001 (MAL-1); Bierne et al., 2003 (EFbis)). However, although diagnostic between species in some areas of the world, these markers may not have universal applicability as diagnostic tools for all three species particularly where true species status may be unclear due to a history of hybridisation and introgression.

In addition to the ecological importance of mussels as members of inter- and sub-tidal communities, all three species are commercially farmed by suspended rope culture (rafts or long-line), bouchots or sea-bed culture and approximately 800 kt of *M. edulis* and *M. galloprovincialis* are produced annually in Europe (Smaal, 2002). Although *M. trossulus* is not exploited in the Baltic Sea (Šmeitanka et al., 2004), this species is cultured in Canada along with *M. edulis* and their hybrids (Penney and Hart, 2002; Penney et al., 2007).

Scottish lochs can provide ideal sheltered sites for rope culture of mussels and there are a number of well-established farms in Loch Etive, Scotland that have at times provided up to 50% of the total production in Scotland. In recent years, these mussel farms have experienced an increasing abundance of mussels with very fragile shells. These are a significant economic problem because the shells are liable to break during post-harvest processing and transport. Such “fragile” mussels also tended to have poor quality meat with grey coloured flesh (Pers comm., D. Fraser). Studies carried out in the early and mid 1990s on growth rates and condition of rope-cultured mussels from Loch Etive did not identify any unusual shaped or fragile shelled mussels (Okumuş and Stirling, 1998; Karayücel and Karayücel, 2000). Indeed, Stirling and Okumuş (1994) report that the shells of Loch Etive mussels were actually stronger and heavier than those from Loch Leven, and this supports the contention that the presence of significant numbers of fragile shelled mussels in Loch Etive is a recent phenomenon.

Here we report on analyses using shell strength, morphometrics, allozyme loci and the Me15/16 locus of samples taken from two Loch Etive mussel rope farms to investigate the distribution and identification of these “fragile” mussels and compare them with the “normal” mussels in the Loch (that are assumed to be *M. edulis*) and samples of *M. edulis*, *M. galloprovincialis* and *M. trossulus* from other locations where their species identity has previously been documented (McDonald et al., 1991).

2. Materials and methods

2.1. Mussel samples and sorting method

Mussels were obtained in May 2006 from two rope-culture mussel farms in Loch Etive, on the west coasts of Scotland, operated by Kames Fish Farming and Muckairn Mussels (Fig. 1, 56° 27' 30" N, 5° 19' 12" W and 56° 26' 55" N, 5° 11' 47" W respectively). Loch Etive has a three basin fjordic structure with several sills distributed along the loch ranging from 4 to 25 m in depth (Edwards and Sharples, 1986). The salinity ranges from 1 to 22‰ at the surface down to approximately 28‰ with a halocline at about 20 m depth (Gage, 1972) and the deep water renewal period is between 1 and 3 years (Edwards and Edelman, 1977).

Two ropes were chosen at random on each farm, one in a central location and one on the outermost header rope furthest from the shore, and samples of mussels were collected from both ropes at depths of 1, 4 and 8 m. Samples were transported live from Scotland to the School of Ocean Sciences, North Wales where they were held in running sea water at 6 °C until analysis.

All the sampled mussels were sorted into three groups, Fragile (FRA), Intermediate (INT) and Normal (NOR), based on visual examination of their external morphology and using a simple test of shell strength. Fragile individuals (Fig. 2) were characterised by elongated “paddle-shaped” shells, with the dorsal and ventral edges being approximately parallel for some of their length. They also had distinctive ridges along the length of the shell. When squeezed gently between finger and thumb along the dorso-ventral axis, the shells showed flexibility and would gape. In Normal mussels the dorsal and ventral edges were seldom parallel for any distance along their length. Normal mussels (Fig. 2) had less pronounced ridges and when squeezed gently the shells offered substantial resistance and were inflexible and would not gape. Intermediate mussels either had elongated paddle-shaped morphology but inflexible shells, or were normal in shape but had flexible shells.

Numbers were counted in each mussel group for each sample and percentage abundance calculated. Mean shell lengths (mm ± SD) over all ropes and farms were 50.4 (±5.1) for fragile mussels, 49.5 (±7.9) for the intermediate group and 48.8 (±6.0) for normal mussels. Sub-samples were then taken for other analyses from each of the sorted groups of mussels.

An independent sample of fragile mussels was taken from ropes on Muckairn Mussels in September 2005 and 25 mg of gill tissue was

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