

Marine invasion genetics: from spatio-temporal patterns to evolutionary outcomes

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Abstract Over the last 15 years studies on invasion genetics have provided important insights to unravel cryptic diversity, track the origin of colonizers and reveal pathways of introductions. Despite all these advances, to date little is known about how evolutionary processes influence the observed genetic patterns in marine biological invasions. Here, firstly we review the literature on invasion genetics that include samples from European seas. These seas constitute a wide array of unique water masses with diverse degrees of connectivity, and have a long history of species introductions. We found that only a small fraction of the recorded introduced species has been genetically analysed. Furthermore, most studies restrict their approach to describe patterns of cryptic diversity and genetic structure, with the underlying mechanisms involved in the invasion process being largely understudied. Secondly, we analyse how

genetic, reproductive and anthropogenic traits shape genetic patterns of marine introduced species. We found that most studies reveal similar genetic diversity values in both native and introduced ranges, report evidence of multiple introductions, and show that genetic patterns in the introduced range are not explained by taxonomic group or reproductive strategy. Finally, we discuss the evolutionary implications derived from genetic patterns observed in non-indigenous species. We identify different scenarios that are determined by propagule pressure, phenotypic plasticity and pre-adaptation, and the effects of selection and genetic admixture. We conclude that there is a need for further investigations of evolutionary mechanisms that affect individual fitness and adaptation to rapid environmental change.

Keywords Europe · Hybridisation · Introduced species · Invasion routes · Cryptic invasion · Population genetics

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Introduction

Evolutionary genetics is a well-established and fertile field of research that has been central for understanding biological invasions (Lee 2002). It has provided the opportunity to unravel concealed patterns and processes involved with species introductions (e.g. Balañà et al. 1994; Taylor and Keller 2007; Cadotte et al. 2009; Lawson Handley et al. 2011) and has boosted contentious scientific debates (e.g. genetic paradox in invasion biology, Tsutsui et al. 2000; Frankham 2005; Roman and Darling 2007). Population genetics, molecular barcoding and phylogenetics are increasingly used to understand aspects of biological invasions such as cryptic diversity, cryptic introductions, tracking the origin of introductions or characterising colonisation pathways (Estoup and Guillemaud 2010; Geller et al. 2010). The term ‘invasion genetics’ was coined in the late 1990s (Villablanca et al. 1998; Davies et al. 1999) and since then invasion genetic studies have proliferated, fuelled by both methodological and analytical advances in genetic techniques (Cock et al. 2010; Reitzel et al. 2013).

As is the case in the field of ecology (Menge et al. 2009), terrestrial and aquatic invasion biology studies have historically progressed in relative isolation (Ruiz et al. 2000; Kolar and Lodge 2001; Grosholz 2002; Callaway and Maron 2006). This may be due to the traditional design of academic pathways or the idiosyncratic and/or antagonistic characteristics of these ecosystems. However, there is no reason to maintain this segregation, as most concepts in invasion biology are applicable across ecosystems (e.g. Roman and Darling 2007; Wilson et al. 2009; Blackburn et al. 2011). Marine ecosystems have a broad range of characteristics that make them ideal model systems for invasion genetic studies. This includes the open nature of the seascape, the diversity of life-histories and dispersal capabilities of marine biota, and the type and frequency of introduction vectors (see details below).

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Holland (2000) produced the first study that specifically reviewed knowledge on marine invasion genetics and detailed the usefulness of genetic techniques for understanding ecological processes involved in biological invasions. More recently, a study reviewing the latest findings in marine invasion genetics emphasized the practicality of genetic tools for the identification of cryptic invasions and sources of introduced populations (Geller et al. 2010). However, to date no review has addressed the link between observed genetic patterns and evolutionary processes in marine biological invasions.

In this review, we begin by examining all available information from invasion genetic studies conducted using samples collected from European seas to assess the state of knowledge and the importance of a number of genetic and life-history traits relevant for colonisation and spread. We chose the marine waters surrounding Europe (northeast Atlantic Ocean and the Baltic, Mediterranean and Black seas) as this region provides an excellent setting to investigate genetic patterns related to marine biological invasions. European shores comprise a wide array of distinct water masses with diverse degrees of connectivity. Also, they have a long history of species introductions—both as a donor and as a receiver (e.g. Patti and Gambi 2001; Roman and Palumbi 2004; Rius et al. 2014). We then analyse how genetic diversity, reproductive strategies and anthropogenic vectors shape invasion genetic patterns. From there we obtain and discuss insights into the evolutionary processes that may underlie biological invasions and how the latest developments in genetic techniques can help to unravel these.

History, regional specificities and genetic patterns of European seas

Inhabitants of the European region, together with southeast Asia, were amongst the first sailors to establish transoceanic routes for commercial and colonisation purposes (Scammell 1981). This represented the dawn of long-distance assisted translocation of marine species. Chinese shipping to the Pacific and Indian Oceans started in the 10th century (Yap and Man 1996) while European shipping traffic to African, American and Asian shores commenced in the 15th century (Scammell 1991), which established global commercial routes. Europe has been the cradle of taxonomy, and as a

result descriptions of marine species from both Europe and abroad emerged in the eighteenth/nineteenth centuries, when transoceanic shipping had already been in place for centuries. Many species that arrived in Europe in historical times were mislabelled as native simply because they were already there when taxonomists came on to the stage (Carlton 2000, 2009). Many purportedly 'European' species are simply early introductions, or should be labelled at best as cryptogenic species (Carlton 1996; Haydar 2012). Consequently, Europe is plagued with historical taxonomic problems and instances of 'pseudoindigenous' species (sensu Carlton 2009). Genetic tools have greatly helped to resolve this issue (Geller et al. 2010), although in some cases the genetic signal has been blurred by centuries of global transportation. Thus, it is nowadays extremely challenging to track the origins and introduction pathways of cosmopolitan species or species complexes (e.g. Zhan et al. 2010; Pineda et al. 2011; Pérez-Portela et al. 2013; Dijoux et al. 2014).

Concerning the geographic particularities of the European region, the NE Atlantic Ocean shores include some of the most frequented shipping harbours worldwide (Kaluzza et al. 2010; Keller et al. 2011). These harbours have provided an extensive and long-term man-made interchange of marine biota among temperate regions, and such exposure to introductions has led to high propagule pressure within the north Atlantic region (Briski et al. 2012). Such large contingents of introduced individuals have resulted in a long list of reported non-indigenous species, often complemented with accurate species range descriptions, but rarely studied in detail retrospectively (how did the introduction and expansion happen?) or prospectively (what are the chances for future introductions?) (but see for example Bolte et al. 2013). Another peculiarity of the European seas is the presence of important semi-enclosed seas, namely the Baltic, Mediterranean and Black seas. These basins are connected to 'outside basins' by extremely narrow links (Kattegat/Skagerrak, Gibraltar, and Sea of Marmara). This particular geographic setting has led some authors to consider these seas as giant mesocosms, whereby the outcomes of 'natural experiments' occurring there have the potential to enhance our understanding of major processes affecting the world's oceans (Lejeune et al. 2010).

The Mediterranean Sea is the most altered and invaded of all European seas, with recent estimates of

the number of introduced species ranging between 500 and 1,000 species (Streftaris et al. 2005; Streftaris and Zenetos 2006; Galil 2009; Coll et al. 2010; Zenetos et al. 2012). The Gibraltar strait represents a strong biogeographic break (Patarnello et al. 2007) and is a hub of human activity, making it difficult to disentangle natural range expansions from human-related species introductions (Rius et al. 2012; Zenetos et al. 2012). The opening of the Suez Canal in 1869 initiated a species migration from the Red Sea to the Mediterranean Sea (the so-called Lessepsian migration) (Streftaris et al. 2005; Galil 2009; Coll et al. 2010). To date more than 330 alien species are considered to have been introduced through the Suez Canal, resulting in a drastic biodiversity change in the Mediterranean Sea (Galil 2007, 2012; Belmaker et al. 2013). However, the perception of the role of the Suez Canal and the Gibraltar Strait as entrance gates may be biased by the failure to recognize early introductions as such (as outlined above), while modern introductions are more easily identifiable. The Lessepsian invasions represent a unique scientific model, as the date of the opening of the Canal is known and the route of invasion is generally unidirectional. Thus, the Lessepsian system allows, within a relatively simple setting, for the testing of specific hypotheses related to the genetics of biological invasions. For example, Lessepsian introductions support the idea that reduction in genetic diversity is not inherent to the invasion process, because since the earliest genetic studies of Lessepsian species, little evidence for genetic bottlenecks has been found (Golani and Ritte 1999; Hassan et al. 2003; Hassan and Bonhomme 2005; Azzurro et al. 2006; Bernardi et al. 2010). In only one instance, namely that of the highly successful introduced bluespotted cornetfish *Fistularia commersonii*, is there evidence of lowered genetic diversity in the Mediterranean Sea (Golani et al. 2007; Sanna et al. 2011).

Contrary to what happens with the Lessepsian connection, the Black Sea and adjacent Azov Sea are naturally connected to the Mediterranean Sea, albeit with extreme restrictions at the Bosphorus and Dardanelles, which are very shallow straits (approximately 50 m in depth) (Yaltrak et al. 2000). Additionally, the influx of freshwater into the Black Sea results in lower salinity compared to the Mediterranean Sea (Sorokin 2002). This translates into the Black Sea waters naturally flowing out towards the Mediterranean, through an upper layer of lower

salinity water, while higher salinity Mediterranean water tends to flow in towards the Black Sea as a bottom layer—similarly to the situation in the Gibraltar strait, where the heavier Mediterranean water flows out towards the Atlantic Ocean (Murray et al. 1991; Sorokin 2002). Due to these particularities, the Mediterranean and Black seas' biota have been isolated with strong limitations to gene flow in place. However, in recent years, changes in the hydrology and abiotic characteristics of the Black sea, together with an increase in ship traffic, have made this natural boundary more permeable (Gregg and Özsoy 2002). Contrary to the Lessepsian situation, the source and route of biological introductions to and from the Black Sea need to be studied carefully, as they may follow different modes. For example, the ctenophore *Mnemiopsis leidyi*, which displays a native range along the eastern seaboard of the United States of America (Reusch et al. 2010), was first recorded in the Black Sea and only later recorded in the Mediterranean Sea (Ghabooli et al. 2011). Genetic studies, based on mitochondrial and nuclear markers confirmed that this ctenophore species was first introduced in the Black Sea (supposedly via ballast water from the Gulf of Mexico, Reusch et al. 2010), and from there invaded the Mediterranean Sea (Ghabooli et al. 2013). These results are consistent with a similar study based on microsatellite markers (Bolte et al. 2013) and, importantly, with the overall hydrography of the region, where surface water (where dispersive propagules are more concentrated) tends to flow out of the Black Sea into the Mediterranean Sea.

Finally, the Baltic Sea includes coastal ecosystems with brackish waters that are considered important centres of xenodiversity (Leppäkoski et al. 2002). The oceanographic similarity between the Black and Baltic seas has led to large scale colonisation pressure of Ponto-Caspian taxa of which representatives of crustaceans (e.g. Cristescu et al. 2004; Cristescu and Hebert 2005; Audzijonyte et al. 2007, 2013) and gobiids (e.g. Brown and Stepien 2008; Feldheim et al. 2009; Neilson and Stepien 2011) have been traced genetically. In some cases, such as with the introduction of the polychaete species *Marenzelleria neglecta*, *M. viridis* and *M. arctia* (Blank and Bastrop 2009), the introduction of non-indigenous species has resulted in significant biogeochemical impacts on coastal ecosystems of the Baltic Sea (Norkko et al. 2012).

Literature review

Table S1 lists 87 studies on invasion genetics (as of 2013, the last full year available) that include samples from European seas, including information on taxonomic affiliations, natural dispersal capabilities, genetic markers used and some major genetic traits. Genetic studies of alien species in European seas started in the 1990s with allozyme analyses, and were subsequently followed by studies using DNA sequence and microsatellite data. Mitochondrial DNA, particularly the cytochrome c oxidase subunit I gene, remains the most widely used genetic marker (44 % of the studies). One surprising result from this review is that after an initial period (1996–2003) of low publication rate (average of 2.3 works per year), the rate increased in 2004 but has since remained fairly constant (average of 7.1 works per year during the period 2004–2013) (Fig. 1a). This is despite a boom in the use of genetic tools in marine research in recent years (e.g. Uriz and Turon 2012).

The geographic areas covered by these studies are depicted in Fig. 1b, showing a predominance of studies covering the NE Atlantic Ocean and the Mediterranean Sea, while smaller areas such as the Baltic and Black seas were the subjects of fewer studies. When we analysed the taxonomic affiliation of studied taxa (Fig. 1c), we found a clear dominance of chordates. Taking as a reference point the taxonomic distribution of alien species reported by Zenetos et al. (2012) in the Mediterranean Sea, the major introduced groups are Mollusca, Crustacea, Polychaeta, Macrophyta, and Fish. Of these, only Macrophyta and Fish have received attention to match their importance in terms of genetic studies (Fig. 1c). In turn, ctenophores, and particularly ascidians, are overrepresented in genetic studies.

The results strongly favour the notion that genetic diversity is not generally impaired when species are introduced. Of the ca. 54 % of studies that did compare genetic diversity in both native and introduced populations, the majority of them (ca. 74 %) found similar diversity in some or all introduced populations. Only ca. 23 % of the studies reported lower genetic diversity in introduced populations, with one study (ca. 2 %) reporting higher diversity in the introduced range (Fig. 1d). Interestingly, when we categorized the dispersal capabilities of the species

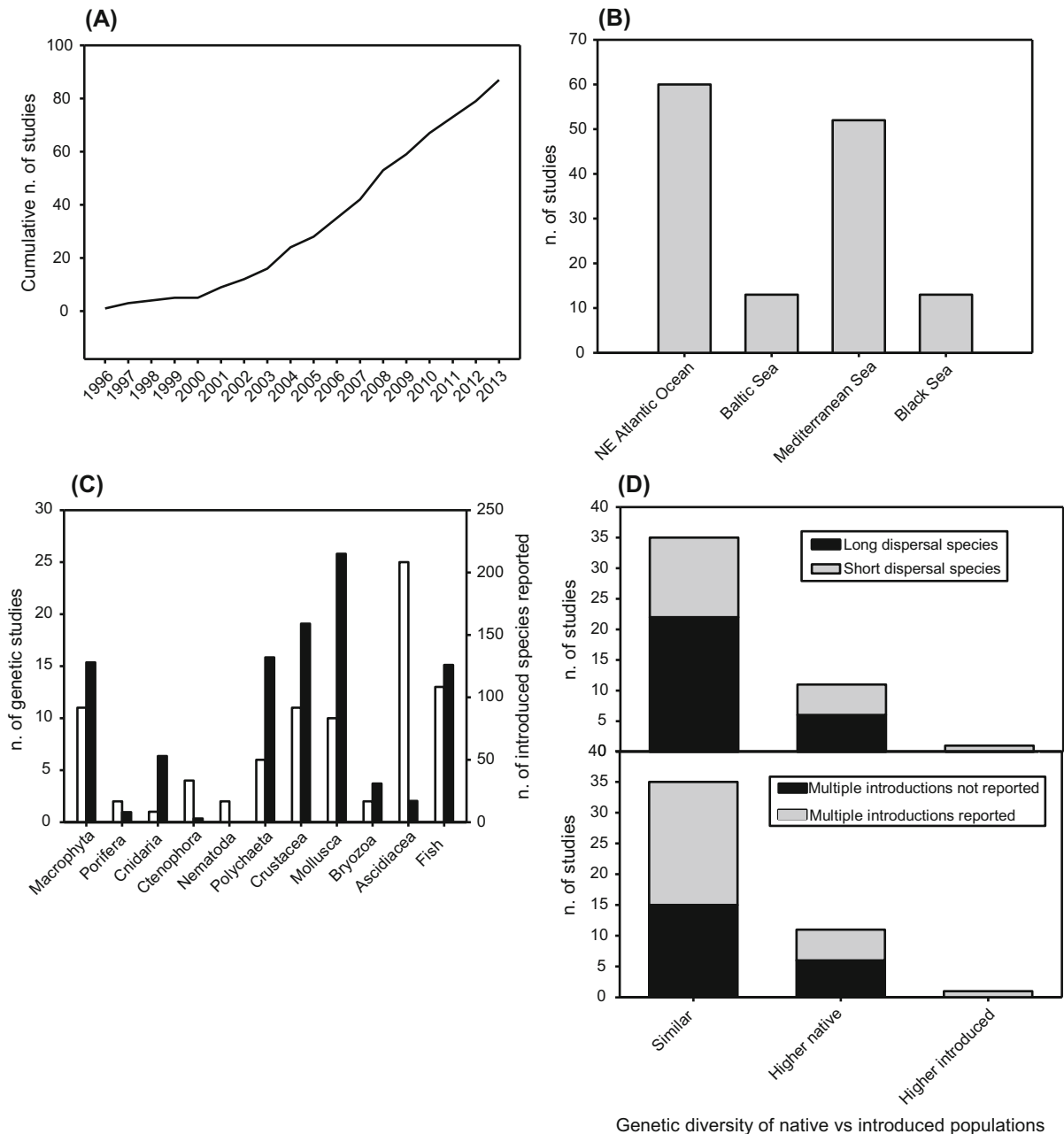


Fig. 1 Genetic studies of marine biological invasions that include samples from European seas (see Table S1 for details). **A** Number of studies over time, **B** number of studies per region, **C** number of species analysed genetically (white bars and left Y axis, note that estimates are conservative: species complexes are considered as a single species, and multispecies works with no clear indication of the non-indigenous status of the species

have been excluded) and number of introduced species reported (black bars and right Y axis, using Zenetos et al. (2012), as a reference), **D** outcome of studies that compare patterns of genetic diversity between native and introduced populations, categorized by offspring dispersal capabilities (short or long, above) and the presence/absence of evidence for multiple introductions (below)

from studies that compare genetic diversity between native and introduced populations into short dispersal (pelagic lifetime less than one week, usually

corresponding to lecithotrophic larvae or direct developers) and long dispersal (pelagic lifetime more than one week, corresponding to long-lived propagules or

planktotrophic larvae), we found that both strategies are represented (Fig. 1d). However, we found a slightly higher frequency of forms with long dispersal abilities in species with similar genetic diversity in native and introduced populations (ca. 63 % vs ca. 55 % of species featuring higher diversity in the native populations). Almost half of the studies in Table S1 (ca. 47 %) reported evidence of multiple introductions. This percentage reaches ca. 57 % in studies reporting similar diversity in native and introduced populations, but drops to ca. 45 % in studies that found higher diversity in native populations. Overall, the evidence from published studies points towards a low frequency of founder effects (i.e. severe genetic drift responsible for a loss of genetic variation after the colonisation of a new site by a limited number of individuals) in marine introductions to European waters, with multiple introductions playing an important role in generating genetic patterns.

As a whole, we found a dearth of genetic studies of European introduced species. Out of an estimated 500–1,000 introduced species (Zenetos et al. 2012), the reviewed genetic studies focussed on only 59 species (or species-complexes). In addition, most studies reviewed here have focussed on resolving cryptic diversity and describing patterns of genetic structure across species ranges, with little work done on adaptive or evolutionary processes.

Genetic diversity, reproductive strategies and anthropogenic vectors

Marine genetic studies routinely encounter a realm full of cryptic diversity (Appeltans et al. 2012). This requires uncovering and understanding a wealth of ecological and evolutionary mechanisms ruling speciation. Studies on marine biological invasions face an additional challenge as a result of human transport, which can determine the distribution of genotypes of species or species complexes (e.g. Daguin and Borsa 2000; Pérez-Portela et al. 2013; Rius and Teske 2013). Even within well-defined genetic lineages, the relationship between genetic diversity and colonisation success has generated an intense debate in the invasion biology literature. Genetic studies consistently show that marine biological invasions are often characterized by the presence of high propagule pressure from multiple and highly divergent sources from the native

range (e.g. Simon-Bouhet et al. 2006; Rius et al. 2012). Another possibility is that the high genetic diversity of localized introduced populations is explained by introductions from a few but genetically highly polymorphic sources (Riquet et al. 2013), a feature that has also been documented in terrestrial populations (Meimberg et al. 2010). Based on these two processes (i.e. introduction from genetically disparate sources or genetically diversified sources), the introduced range generally has similar or higher mean values of genetic diversity than the native range (e.g. *Crepidula fornicata*, Fig. 2). However, there are exceptions to this (Koskinen et al. 2002; Gaither et al. 2012) and key population processes such as genetic bottleneck, genetic drift, lag period and/or Allee effects (Tsutsui et al. 2000; Leung et al. 2004; Crooks 2005; Dawson and Hamner 2005; Taylor and Hastings 2005) can be responsible for reducing levels of genetic diversity. Some studies on marine introduced species have indeed reported low levels of genetic diversity (e.g. Provan et al. 2005; Dupont et al. 2007b; Golani et al. 2007; Tepolt et al. 2009; Pérez-Portela et al. 2012; Rius and Shenkar 2012). In some species, strong founder effects during expansion may result in a decrease in genetic diversity over time (e.g. *Perophora japonica*, Pérez-Portela et al. 2012) or create an expansion wave (see Ciosi et al. 2011 for a terrestrial example). It has been shown that such low levels of genetic diversity do not generally compromise population establishment and the spread of non-indigenous species (Roman and Darling 2007). Some studies report a complex interplay of primary and secondary introductions (also called pre-border and post-border stages, see Forrest et al. 2009), with the former transfer happening unidirectionally (from the native to the introduced range), while the latter occurs within the introduced range. In such cases, the native range is normally characterized by a well-defined genetic structure while the introduced range is diverse but highly homogenous (Voisin et al. 2005; Simon-Bouhet et al. 2006; Rius et al. 2012). When human-mediated transport results in bi-directional relocation of propagules between the native and introduced ranges, a random reshuffling of genotypes occurs, which may lead to global genetic homogenisation (Zhan et al. 2010; Pineda et al. 2011).

When genetic attributes are compared among species with different reproductive strategies, common outcomes can be found. For instance, both poor

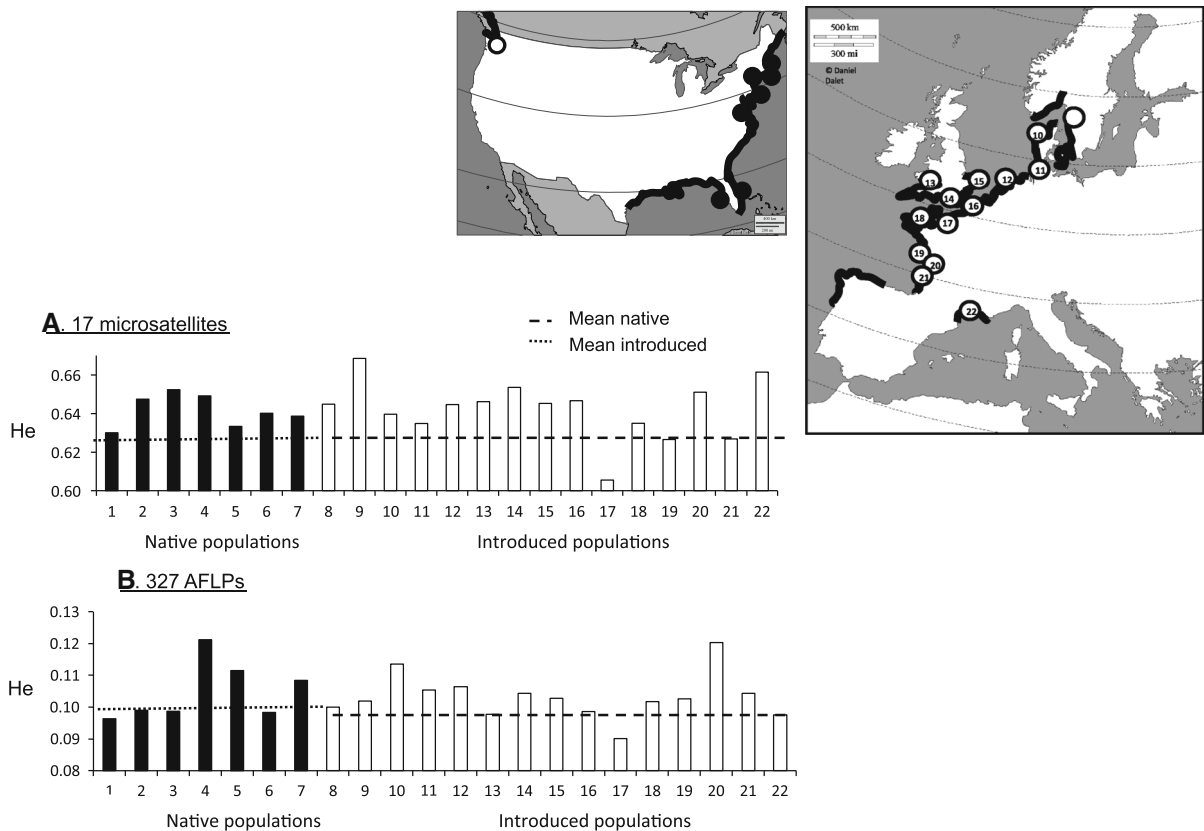


Fig. 2 Genetic diversity using: **A** 17 microsatellites and **B** 327 AFLP loci from native (*black bars*; NW Atlantic) and introduced (*white bars*; Mediterranean Sea, NE Atlantic and NE Pacific) populations of *Crepidula fornicata*. Different styles of *dashed lines* represent mean diversity across all populations of the native and introduced ranges respectively. Comparisons

of genetic diversity among native and introduced populations yield non-significant differences ($P = 0.99$ and 0.85 for microsatellites and AFLP, respectively, based on a permutation test, 5,000 permutations of individuals between groups). Sources of the introduction are presumably located in the northern part of the native range. Data from Riquet et al. (2013)

dispersers, such as direct-developers (e.g. the gastropod *Cycolope neritea*, Simon-Bouhet et al. 2006) or species with lecithotrophic larvae (e.g. the ascidian *Microcosmus squamiger*, Ordóñez et al. 2013), and highly dispersive species, like benthopelagic species with long-lived larvae (e.g. the gastropod *C. fornicata*, Riquet et al. 2013 and references therein), are all successful invaders that show no reduction in genetic diversity compared to the native range. This is counterintuitive as in the absence of human-mediated transport of species, short and long planktonic larval duration display different dispersal kernel distributions and thus dissimilar genetic dispersal estimates (Siegel et al. 2003). Differences may be expected when considering social organisation or gregarious behaviour. For instance, colonial vs. solitary ascidians

were shown to display contrasted genetic patterns in their native range (Ayre et al. 2009). And yet, both colonial and solitary non-indigenous species show similar genetic patterns (Bock et al. 2011; Goldstien et al. 2011; Bock et al. 2012; Rius et al. 2014). Taken together, genetic studies analysing the role of reproductive strategies of introduced species suggest that these different strategies have little effect on the composition and distribution of genetic signatures.

The open nature of most seascapes prevents the efficient containment of introduced marine species and facilitates the spread of initial and successive waves of founders in the wild. Such spread has been demonstrated using bio-physical modelling of the larval dispersal of *C. fornicata* in its European introduced range (Viard et al. 2006; Dupont et al.

2007a). Furthermore, the long-lived larval stages of many marine organisms allow them to typically remain in the water column for a few weeks (Shanks 2009), which might be an advantageous trait in artificial transportation (e.g. ballast waters). In addition, organisms can survive long periods of transport time (e.g. several months for the benthic amphipod, *Corophium acherusicum*, in ballast water tanks, Gollasch 1996). In yet another instance, Gollasch et al. (2000) showed that the abundance of the copepod *Tisbe graciloides* grows exponentially in ballast waters irrespective of transport time and species diversity. Anthropogenic vectors (e.g. ballast waters, aquaculture, and fouling of ship hulls and sea-chests) represent highly efficient ways to transport large numbers of individuals per species and an array of species (Carlton and Geller 1993; Cohen and Carlton 1998; Carlton 2001). Similarly, marine infrastructures (i.e. man-made mobile or immobile structures) have been identified as major vectors for both primary introductions and subsequent expansions (i.e. stepping stones, corridors or bridgehead effects; Bulleri and Airoidi 2005; Dafforn et al. 2009; Mineur et al. 2012). However, studies comparing different vectors are lacking. For example, ballast water is known to be very effective at transporting invertebrate larvae but most likely plays a minor role in the transport of fish species (with the notable exception of the round goby, *Neogobius melanostomus*, introduced from the Black Sea to the Great Lakes, Fuller et al. 2014). Ship fouling is a non-selective vector for non-indigenous benthic species, particularly those that take refuge in sea chests and other structures less exposed to drag during navigation (Coutts and Dodgshun 2007). In another notable instance, recreational boating is an important vector for the spread of non-indigenous species (Acosta and Forrest 2009), specially during the secondary stage of introduction (Mineur et al. 2008). This vector remains the largest unregulated vector for the introduction and spread of marine non-indigenous species (Clarke Murray et al. 2011).

Population genetic studies have revealed interesting patterns of introduction and spread via aquaculture. This vector is believed to account for as many introductions as shipping (Savini et al. 2000; Wolff and Reise 2002; Streftaris et al. 2005; Mineur et al. 2007). Contrary to the somewhat haphazard role of shipping, aquaculture is particularly prone to repeated introductions due to the continued interchange of

species among facilities. For instance, the rapid spread of the gastropod *C. neritea* along the French Atlantic coasts was shown to be associated with an admixture event between divergent genetic lineages, which increased genetic diversity in the newly recorded French populations (Fig. 3). Such a pattern is best explained by recurrent introductions from several areas in the Mediterranean Sea, including important shellfish culture sites in Spain, France and Italy (Simon-Bouhet et al. 2006). Another instance is the Japanese kelp *Undaria pinnatifida*, which is native to Asia and was first accidentally introduced in the Thau lagoon (French Mediterranean Sea) in the 1970s and subsequently intentionally transported to NE Atlantic shores to be cultivated. Genetic studies have shown that sustainable populations can be established after their escape from aquaculture facilities (e.g. in the English Channel, Grulois et al. 2011). The cultivated origin of wild populations of *U. pinnatifida* is supported by evidence that cultivated and wild populations belong to the same genetic lineage (Voisin et al. 2005). The escape and sustainable establishment of cultivated stocks has also been clearly demonstrated for the Pacific oyster *Crassostrea gigas* in Ireland (Kochmann et al. 2012). For both the Japanese kelp and the Pacific oyster, genetic data strongly suggest that wild populations have become self-sustainable. Another type of introduction derived from aquaculture activities concerns escapes of domesticated fish and their associated fauna, which in some cases has fully replaced native populations or have become introgressed with native populations (e.g. Glover et al. 2013). Such processes may, in addition, facilitate the translocation of non-indigenous pathogens to native species. This is exemplified by the large-scale infestation of the European eel *Anguilla anguilla* by the Asian parasite *Anguillicola crassus*. This is despite the fact that its original host (*Anguilla japonica*) has never successfully established in European waters (Wielgoss et al. 2008).

New regulations and international conventions aimed at controlling the transport of marine species (e.g. European Community No. 708/2007 of 11 June 2007 concerning the use of alien and locally absent species in aquaculture, or the new European Union 2020 Biodiversity Strategy that proposes a firm commitment to protect biodiversity and mitigate introduced species that threaten important economic activities) will contribute to the constraint of future

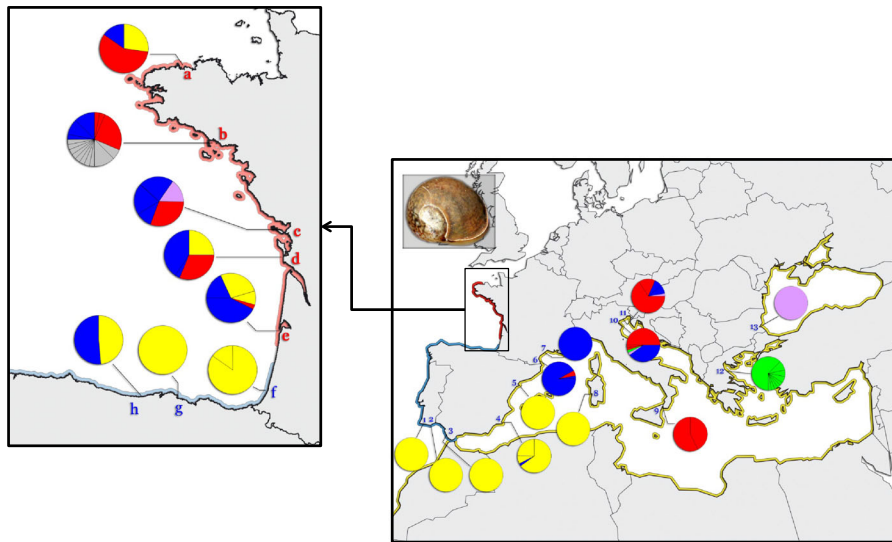


Fig. 3 Increased genetic variance and admixture between genetically divergent lineages of *Cyclope neritea* in the NE Atlantic introduced range (red line in left map; population samples a–e) as compared to its native range in the Mediterranean and Black seas (yellow line; samples 1–13). Ephemeral populations are also documented along the Iberian Peninsula

(blue line, samples f–h). Circles show the frequency distribution of mitochondrial haplotypes at population level. Colours indicate different groups of divergent haplotypes. Details are provided in Simon-Bouhet et al. (2006), bar for two populations (Aegean and Black seas, green and violet pie charts, respectively) that are included here but were not analysed in the paper

introductions. However, it is uncertain how these measures will affect genetic patterns of non-indigenous species.

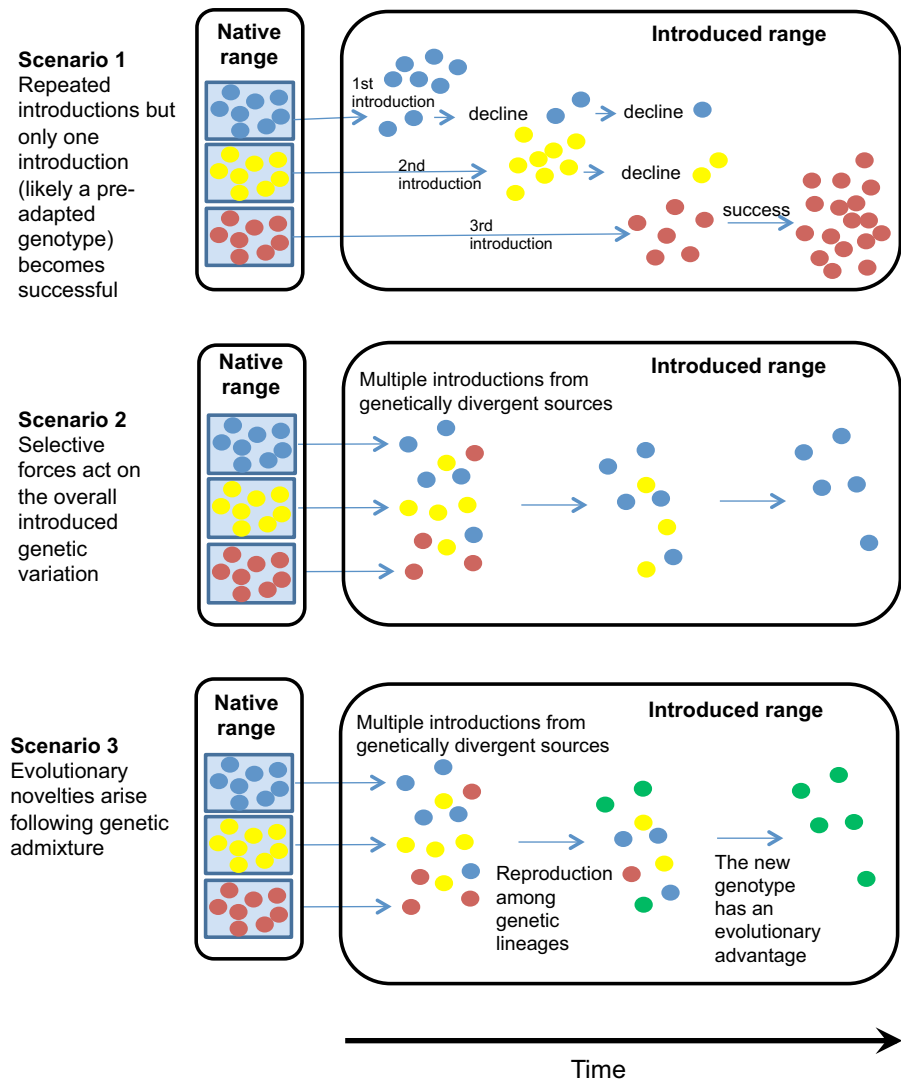
Evolutionary outcomes

As seen above, studies of successful marine non-indigenous species routinely report the presence of populations with high genetic diversity in the introduced range. This situation may be linked to evolutionary neutral or selective processes. In the simplest case, all introduced genotypes establish and spread in the new environment, which can be similar to the native range. If the environment in the native and introduced range differs, phenotypic plasticity may be responsible for counteracting any effect of environmental filtering (Emerson and Gillespie 2008; Davidson et al. 2011). Phenotypic plasticity is a heritable trait that can accelerate adaptive processes (e.g. genetic assimilation, Lande 2009; Fierst 2011). As introduced populations face important selective constraints and pressures over contemporary time scales (Huey et al. 2005), selection acting on the genetic background of introduced individuals is likely to be

important (Novak 2007). In such cases, a central question arises: what are the evolutionary mechanisms based on selective processes that promote the sustainable and successful establishment of populations of non-indigenous species? Three possible explanations are proposed for selective processes occurring during the introduction of multiple divergent genotypes into a new range (Fig. 4).

The first scenario considers a situation whereby the introduced range receives introductions from divergent genetic backgrounds but only one of them establishes (e.g. exclusion as a result of environmental filtering). The successful genotype may be better adapted to the new environment (often called ‘pre-adapted’ genotype, see Dlugosch and Parker 2007). This scenario requires some sort of match between conditions in the environment of the new range and the evolutionary processes that occurred over long periods of time in the native range (Facon et al. 2006). This situation has been reported in some studies of marine systems. For instance, cryptic invasions by an introduced lineage were the most likely explanation for a new rapid expansion of *Carcinus maenas* along the NE Pacific shoreline (Roman 2006; Tepolt et al. 2009). This ‘failure-success’ scenario is difficult to

Fig. 4 Potential selective processes acting during the introduction of multiple genetically polymorphic and/or divergent sources. Each *colour* represents individuals with a specific genetic background from the native range that may be neutral, adaptive or deleterious in the introduced range. *Squares* in the native range feature genetically divergent groups of individuals along the species range. *Arrows* in the introduced range represent temporal changes. Note that the first scenario includes temporally sequential introductions but that the same outcome may occur when the three genotypes are introduced at the same time



prove without regular temporal surveys and specimen collections, including sampling from early or unsuccessful introductions. Museum collections and/or herbarium specimens (e.g. Lees et al. 2011) are of primary interest to resolve this point. Studies of failed introductions and monitoring invaders over time (e.g. survey of ‘boom and bust’ dynamics) are crucial for understanding long-term invasion dynamics (Suarez et al. 2005; Strayer et al. 2006; Pérez-Portela et al. 2012) although opportunities to study such events are rare.

The second possible scenario (Fig. 4) involves selection forces that affect the standing genetic variation (i.e. pre-existing polymorphisms)

introduced from the native range. This scenario mimics a situation often encountered in marine invertebrates with: (1) high genetic diversity and structure in the native range, and (2) high propagule pressure following the introduction process. Interestingly, scenario 2 differs from scenario 1 in that introductions from isolated regions of the native range are not required. Introduction may simply occur from a genetically polymorphic source, and subsequently selection (e.g. through competition and predation) would follow. Selection on pre-existing polymorphisms may operate over short time scales compared to selection on new mutations (Barrett and Schluter 2008; Vandepitte et al. 2014). The genetic

variants on which selection operates in the introduced range may be neutral or even slightly deleterious in the native range but confer some advantage to the introduced individuals in their new environment. Genome scans are appropriate methods to detect loci influenced by selection processes (i.e. outliers) in the absence of knowledge about the genes and traits that may be under selection (Bierne et al. 2011). Using such an approach, Riquet et al. (2013) did not find any outlier loci when comparing native American and introduced European populations of the slipper limpet *C. fornicata*, while their study revealed outliers between populations in the native range. This outcome suggests that either no selection on standing genetic variation occurred following the introduction process or, simply, that genome scans, particularly when using a low number of markers, may not be efficient for identifying selection during colonisation (short time elapsed since the introduction). In contrast, Rohfritsch et al. (2013) showed the existence of outlier loci in introduced European populations of the Pacific oyster *C. gigas*. Two groups of populations were identified based on some of the outliers, but such genetic structure was uncorrelated with the one observed from neutral loci. While the authors did not fully exclude the effect of secondary multiple introductions, they suggested that parallel adaptations occurred in similar environments (in this case fjord-like environments). The two examples detailed above advocate for further investigation of the adaptive genomic architecture of native and introduced populations.

The last selective evolutionary scenario (Fig. 4) is based on the idea that new adaptive genetic combinations could arise from intraspecific crosses among individuals characterized by different genetic backgrounds (Facon et al. 2008; Lawson Handley et al. 2011). Similarly to interspecific hybridisation (Ellstrand and Schierenbeck 2000; Seehausen 2004; de Carvalho et al. 2013), genetic admixture may create novel allelic combinations that enhance the fitness of introduced individuals. The underlying rationale is that new heritable traits arise because of novel genetic combinations and that selection operates on these new traits (Rius and Darling 2014). In the same way as heterosis (or hybrid vigour) among interspecific lineages operates (e.g. Drake 2006), strong evidence of correlation between genetic admixture and fitness of introduced individuals has been shown (e.g. Kolbe

et al. 2007; Turgeon et al. 2011). Although the consequences of genetic admixture of divergent genotypes have been rarely studied in marine systems, studies reporting genetic admixture in introduced populations are proliferating. Pineda et al. (2011) found an excess of admixed genotypes of two nuclear lineages in introduced populations of the ascidian *Styela plicata*, which suggests that selection favours novel genetic combinations. Similarly, introduced populations of other widespread ascidian species show genetic admixture of divergent lineages (Rius et al. 2012; Zhan et al. 2012). However, this does not necessarily mean that admixed genotypes are always favoured in the introduced range, as the predominance of unadmixed genotypes has also been reported (Ordóñez et al. 2013).

Taken together, pre-adaptation, selection on standing genetic variation and genetic novelties arising from post-immigration genetic admixture can be important drivers influencing evolutionary outcomes. Further research should yield important insights about these mechanisms in marine introductions.

Concluding remarks and future directions

Studies on marine invasion genetics have generally shown that introduced populations rarely suffer from founder effects and are characterized by high genetic diversity, most likely as a result of repeated introductions and high propagule pressure. Despite almost 20 years of research, our study suggests that marine invasion genetics is still in its infancy. Most studies in European seas have focussed on cryptic diversity and descriptive comparisons of genetic composition and structure, from which insights into introduction patterns (pathways, sources, connectivity, etc.) have been drawn. However, little information is available on the underlying evolutionary mechanisms involved in marine biological invasions.

The currently limited genetic information of marine non-indigenous species makes the link between genetic information and rapid adaptation, phenotypic plasticity or fitness, elusive. The lack of comprehensive associations between genetic diversity and the success of marine biological invasions also brings into question the plausibility of using neutral genetic diversity as a proxy for adaptive genetic diversity and colonisation success (Hansen et al. 2012). The

patterns observed to date advocate for further investigation of genetic and genomic architecture of marine non-indigenous species as well as in-depth analyses of the link between genotypes and phenotypes, considering in particular the fitness and adaptive potential of admixed genotypes.

Key concerns such as the introduction history and the traits that determine invasiveness of non-indigenous species may benefit immensely from major advances in molecular biology and bioinformatics. Issues related to phylogeny and identification, historical and contemporaneous sources of non-indigenous species, population characteristics, and potential or realised adaptation can be tackled through an increasingly sophisticated analytical toolbox (reviews by Allendorf et al. 2010; Cock et al. 2010; Angeloni et al. 2012). The advent of next generation sequencing techniques (NGS) has revolutionized the potential for genetic and phenotypic analyses of the invasion process in non-model organisms. New markers such as single nucleotide polymorphisms (SNPs) can be easily developed from sequence data of full or partial genomes or transcriptomes (Everett et al. 2011; Helyar et al. 2011; Seeb et al. 2011; Reitzel et al. 2013). They allow for precise population genetic analyses, while at the same time allowing for the detection of adaptive changes through the study of outlier loci with non-neutral behaviour (Stapley et al. 2010; Rohfritsch et al. 2013). NGS methods allow the study of hybridisation patterns of sibling species in secondary contact zones (e.g. Blank et al. 2012). They also enable the study of global gene expression patterns through so-called RNA-seq techniques (Wang et al. 2009; Wolf 2013), which can highlight differential expression levels of key genes as a response to new conditions in the introduced range. NGS techniques are also being increasingly used in the study of environmental DNA for several applications (Bohmann et al. 2014). Among these, environmental DNA can be a powerful tool for the early detection of introduced species, even before they become conspicuous in new localities (Bott et al. 2010; Bucklin et al. 2011). Another promising technique involves the sequencing of ancient DNA and historical (often low quality) DNA, which is highly applicable to museum collections that harbour alien taxa (e.g. Roman 2006; Lees et al. 2011). Finally, it is increasingly recognized that epigenetics, the study of heritable changes in gene expression and function that cannot be explained by

changes in DNA sequence, affects the phenotype and hence the potential to adapt. This happens through changes in the DNA methylation status, remodelling of chromatin structure and the regulation of expression mediated by microRNA (Bossdorf et al. 2008 and references therein). Such routes have yet to be explored in marine non-indigenous species, but may provide the key to understanding factors affecting invasiveness.

Overall, the combination of genome-, transcriptome- and proteome-based methods will increasingly facilitate the investigation of a large set of issues in biological invasion studies; from the identification of non-indigenous species to the disentangling of the roles of phenotypic adaptation versus evolutionary change in the success of introductions. Much remains to be done for molecular techniques to become fully implemented in invasion genetics, especially with regards to describing and understanding the evolutionary mechanisms involved in the invasion process in marine ecosystems.

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