What is natural?
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Synthesis

Deniz Haydar
In this thesis the extent to which natural patterns of diversity and distributions in coastal marine ecosystems have been affected by biological invasions is examined. In Part I, the focus is on established non-indigenous and cryptogenic species, the magnitude of invasions and the predominant vectors in the North Sea.

**Introduced species in the North Sea**

The number of introduced and cryptogenic species known from the North Sea region (**Chapter 2**) has doubled since the previous checklist of 1999 (Reise et al. 1999), amounting to 167 introduced and cryptogenic species. This increase in the number of invasions in the North Sea is not entirely due to newly arriving invaders, but is also the result of the inclusion of previously overlooked invasions and cryptogenic species. Not all of these introduced species are known to have established in the North Sea; only 124 non-indigenous and cryptogenic species have actually established self-sustaining populations. Paleoenvironmental history (post-glacial recolonization of the North Atlantic in general and of the North Sea in particular) and disturbance due to strongly transformed modern coastal environments have contributed to relatively low species richness in the North Sea. This may be one of the explanations of the high number of introduced species. Many of the species that were introduced became established, increased local diversity and considerably modified ecosystem functioning in the nearshore zone (Reise et al. 2006). Matching the world-wide pattern, the rate of invasions has increased in the North Sea (Reise et al. 1999), and it will probably continue to increase as a consequence of climate change and ongoing globalization.

The majority of non-indigenous and cryptogenic species have localized distributions; only ten of these are known from all seven countries bordering the North Sea. However, continuing shipping and shellfish translocations may result in rapid secondary spread of these introduced species to other North Sea coasts and beyond. The checklist of non-indigenous and cryptogenic species presented in Chapter 2 may serve as a basis for future studies; it will have to be periodically updated with newly arriving invaders and spreading established invasions. New introductions will inevitably occur and established introductions will spread by natural or anthropogenic means in the coming years. In Chapter 2 the number of cryptogenic species is severely underestimated because only those species were included for which there is a strong indication that they were introduced in some part of their range, but for which the origin remains unknown. The actual list of cryptogenic species is undoubtedly much longer (see Chapter 4).

The effect of invasions in the North Sea was not the subject of this chapter, but three case-histories of non-indigenous species with significant ecological and economic impact on coastal systems in the North Sea were presented in addition to the checklist of introduced species. The slipper limpet *Crepidula fornicata*, the Chinese mitten crab *Eriocheir sinensis* and the shipworm *Teredo navalis* are examples of well-known and extensively studied non-indigenous species. For the majority of non-indigenous
species the impact on North Sea ecosystems remains unknown due to the lack of scientific studies on the effect of invasions in this region.

The predominant vectors for introduction of non-indigenous species in the North Sea are hull fouling and aquaculture (in particular oyster translocations), which are each responsible for 25% of the total number of introduced species.

**Oysters as a vector**

Oyster transports are one of the strongest vectors in the North Sea (Chapter 2), and in Dutch coastal waters. In Chapter 3, a detailed analysis of this vector was presented in order to explain its high share of introductions into The Netherlands. The frequency and scale of oyster translocations and the characteristics of this vector - the rugged shells of oysters offer ample opportunities for epiflora and -fauna to settle and survive transport to other regions - may explain the relatively high number of oyster-associated introductions, and were investigated here.

A literature review of oyster-associated species introductions resulted in a list of 35 non-indigenous oyster-associated species that have become established in The Netherlands. Of all associated introductions 45% originate from the Northwest Pacific and most these are assumed to have been introduced with Pacific oyster (*Crassostrea gigas*) imports. Some may have been introduced with hull fouling to Europe and have subsequently spread in European waters with oyster transports. The Northwest Atlantic is the origin of 20% of oyster-associated introductions; these species are supposed to have been introduced with shipments of the American oyster *C. virginica*.

The increased rate of oyster-associated introductions in the past 30 years is consistent with world-wide patterns of increased introduction rates, but does not coincide with increased commercial oyster imports. Instead the oyster import data, obtained from Statistics Netherlands (CBS), show a decrease in the amount of oysters imported since the 1970s, in particular of seed oysters or smaller oysters, which are imported to restock local culture. However, not all oyster imports are reported to the authorities. *C. gigas* is known to have been introduced to The Netherlands in the 1960s directly from Japan and via British Columbia (Shatkin *et al.* 1997; Drinkwaard 1999; Wolff & Reise 2002), but we did not find any official records of these imports. Unreported translocations of oysters are suspected to occur in other countries as well (Verlaque 2001), and the patterns of secondary spread of associated non-indigenous species provide evidence of ongoing transports. Even though adult oyster imports that are currently occurring may not be intended for restocking local oyster culture, the oysters may still be relaid on culture plots or in basins on the shore from where the introduction and secondary spread of associated species is still possible.

In Dutch coastal waters, the Pacific oyster has formed extensive intertidal and subtidal reefs that are continuing to increase in size. *C. gigas* is being cultured on plots in the Oosterschelde estuary. In order to analyze oysters as a vector, we collected and identified the epiflora from live Pacific oysters from these culture plots that were
treated as if they were transported to other European culture sites for relaying. Red seaweeds were the most common group of macroalgae retrieved from the oyster shells, and they also constituted the largest fraction of species introduced with this vector. The oyster shells provided a substrate for 41 macroalgal taxa, of which 36 were identified to species level. These macroalgae were native, cryptogenic and non-indigenous species; of the most common species, 50% were introduced. A single oyster may harbor up to 14 macroalgal taxa, the maximum species richness on oysters from the Oosterschelde estuary was estimated to be 44 species of macroalgae. Relatively small numbers of oysters (~500) may carry large numbers of associated species and individuals, resulting in a high potential of introducing non-indigenous species. The introduction of these species with their substrate further facilitates their establishment, which may partly explain the increase in oyster-associated introductions in the past decades.

Furthermore, the rapidly growing Pacific oyster reefs form a new habitat for fouling species in The Netherlands, and are likely to facilitate the establishment of associated non-indigenous species, possibly accelerated by other factors such as climate change and increased disturbance in the recipient region.

Pacific oysters in the Oosterschelde estuary are a substrate for native and introduced species, and for a large number of cryptogenic species. Historical introductions with oyster transports may have resulted in cosmopolitan or disjunct distributions of species we now call native, as pre-19th century movements of non-indigenous and native species with oysters within Europe are likely to have occurred. Oyster-associated introductions are not only a phenomenon of the past: the ongoing shellfish movements within Europe contribute to introduction and rapid secondary spread of non-indigenous species, and to exchange between populations of native and cryptogenic species. Oyster translocations are thus blurring natural distribution patterns and homogenizing diversity of algae and invertebrates in coastal waters.

The scale of cryptogenesis

Part II of this thesis is devoted to the scale of cryptogenesis in the North Atlantic Ocean. In general, the share of invasions is hypothesized to be highly underestimated (see Chapter 1), because species are assumed to be native, unless they are proven to be introduced. Regional checklists of introduced species often include cryptogenic species (see Chapter 2), but the cryptogens in these checklists are very likely to have been introduced, although their origin remains unknown. In Chapter 3, many of the macroalgae occurring on oyster shells were assigned to the cryptogenic species category, based on their association with anthropogenic vectors (oysters and hull fouling), and their disjunct or cosmopolitan distribution patterns. Although large-scale shipping across the Atlantic had been taking place long before the first comprehensive biological surveys were conducted, in contemporary marine ecology historical invasions are generally ignored, assuming that the 19th century coastal biota was natural or indigenous (Carlton 1989; 2003b).
Cryptogenic species are by definition all species that are neither demonstrably native nor introduced (Carlton 1996), and include species that are falsely viewed as native. In order to get a more robust estimate of the number of cryptogenic species, in Chapter 4 lists of all reported species from three taxonomic groups of shallow-water invertebrates in the North Atlantic Ocean were compiled. For each species, not only world-wide distribution data were included, but natural dispersal potential, habitat characteristics and association with anthropogenic vectors were also noted. The three taxonomic groups that were analyzed (Asciidacea, Hydrozoa and Bivalvia) differ in their natural dispersal potential. Asciidacea are poor dispersers with a short pelagic larval phase. Hydrozoa have a high dispersal potential: they have pelagic larvae, sometimes a free-swimming medusa and the polyps may be able to raft. Bivalvia have a long-lived larval phase; they can be divided in three groups: infaunal bivalves, that are able to disperse only via pelagic larvae, and epifaunal- and boring bivalves, both of which may additionally be able to raft. All groups except most infaunal bivalves are potentially dispersed as ship hull fouling. The infaunal bivalves were used as a control group, because it was hypothesized that all introductions of infaunal bivalves are known since they are likely to have mostly occurred with ballast water, which has only been in use since 1870. Thus, unknown historical introductions are not expected to occur in infaunal bivalves.

One of the characteristics of cryptogenic species is a disjunct distribution pattern, which we used as a proxy for cryptogenesis. A disjunct amphi-Atlantic distribution pattern, defined as a distribution pattern that spans European and American North Atlantic coasts, but is interrupted in Arctic or sub-Arctic waters, can be explained by four scenarios: natural trans-oceanic dispersal, post-glacial recolonization, cryptic speciation and human-mediated introductions. Literature on the four proposed scenarios was reviewed and relative numbers of cryptogenic species were compared among and within groups with disjunct amphi-Atlantic distributions.

Natural dispersal by either planktotrophic larvae or rafting on various substrates does not explain disjunct amphi-Atlantic distribution patterns of individual species of Hydrozoa, Bivalvia and Asciidacea. Dispersal by these mechanisms is highly unlikely and has not been demonstrated for any organism in the North Atlantic Ocean. Additionally, based on the surface-current regime the direction of transport would have to be from west to east, which is in conflict with patterns of migration and invasions in the North Atlantic Ocean.

Infaunal bivalves have the lowest proportion of disjunct amphi-Atlantic distributions (10 out of 299 species). There are no cryptogenic infaunal disjunct amphi-Atlantic bivalves, nor are there infaunal bivalves that have a disjunct amphi-Atlantic distribution that can be explained by pelagic larval dispersal. The disjunct distributions of infaunal bivalves are either explained by known anthropogenic introductions, or by other factors, such as occurrence in deep or warm waters. In Hydrozoa, a free-swimming medusa does not guarantee long-distance dispersal and a wide, possibly disjunct, distribution. Rafting may be a possible mechanism for regional dispersal of Hydrozoa, but those species that are able to raft are also likely to be able to attach to
ships. Long-distance dispersal is more effective on ships than on rafts; ships travel fast, are independent of surface currents, provide more space and travel farther.

Cryptic species are common in all taxonomic groups and could explain some of the disjunct amphi-Atlantic distributions, as has previously been shown for several invertebrate species.

The role of Pleistocene glaciations in the creation of disjunct amphi-Atlantic distributions is assumed to be the same for all groups. However, there are no infaunal bivalves with a natural disjunct distribution pattern, nor are there cryptogenic infaunal bivalves. Additionally, for none of the groups do studies exist that give conclusive evidence for a disjunct amphi-Atlantic distribution pattern that is the result of post-glacial dispersal across the North Atlantic. It is difficult to distinguish between genetic diversity patterns caused by the LGM and by an anthropogenic invasion, as both processes can result in either high or low levels of genetic diversity (see Chapter 5). There is only one example of a species with a natural disjunct amphi-Atlantic distribution in the North Atlantic Ocean (*Mytilus edulis*), but this species may actually have an amphi-Atlantic distribution pattern. There are no other examples of naturally disjunct amphi-Atlantic distributions that have been demonstrated using a combination of phylogeographic, palaeobiological and historical data.

Disjunct amphi-Atlantic distributions are not common: 10% (108 species) of all shallow-water species of Ascidiae, Bivalvia and Hydrozoa (n = 1054) have a disjunct distribution pattern, and about half of these are categorized as cryptogenic (38 species) and introduced species (22 species). The other half include species that also occur in deep or warm waters, species complexes, species with disjunct distributions that are based on single or doubtful records on either coast, or species of which the taxonomy is uncertain, and may therefore not be truly disjunct amphi-Atlantic species. For 8 species the disjunct distribution appeared to be natural.

The proportion of disjunct distributions differs among groups with differing life-history characteristics and relative natural dispersal potential, and ranges from 3% to 48% (Table 6.1). The relative number of cryptogenic and known introduced species within the disjunct amphi-Atlantic category ranges from 1.3% to 28% of the total number of species per group. This wide range of relative numbers is caused by differing dispersal potential of the studied groups, which were selected for the reason that they span a large part of the “natural dispersal scale”. For the epifaunal groups (i.e. all groups except the infaunal bivalves), the relative number of cryptogenic species ranges from 1.3% to 24% of the total number of species per group. This could amount to at least 38 overlooked invasions of ascidian, bivalve and hydrozoan species. Extrapolating this to all invertebrates and macroalgae in the North Atlantic Ocean, this suggests that between 1.3% and 24% of the shallow-water epifaunal flora and fauna is cryptogenic and may historically have been introduced; hence, the number of overlooked invasions could be of the order of magnitude of hundreds of species. This is still a conservative estimate: we have only considered species with a disjunct amphi-Atlantic distribution, although species occurring on either Atlantic coast or with a continuous amphi-Atlantic distribution may also be cryptogenic or introduced.
The traditional assumption of limited influence of historical shipping on dispersal of coastal organisms has great implications for understanding modern-day distributions of species in North Atlantic waters. The estimated 1.3 to 28% of species that may have been introduced is not limited to inconspicuous species, rare species or species playing a minor role in coastal communities. Key species of coastal communities may have been introduced by ships centuries before the onset of biological surveys, but are now falsely viewed as native (Carlton 2003b). Known anthropogenic introductions of key structuring taxa are resulting in similar faunas on both sides of the Atlantic, blurring some of the key differences in assemblage composition and community organization (Jenkins et al. 2008). The perception of the natural state of the system has shifted: historical introductions are regarded as natural components of the studied community. Assigning species the cryptogenic status creates possibility for further studying the scale of historical invasions. A multidisciplinary approach, combining palaeoecological, archaeological and historical resources, as well as molecular techniques is essential in order to gain insight into the scale and consequences of marine invasions.

Table 6.1 Summarized numbers and relative numbers (between brackets) of species with disjunct-amphi Atlantic distribution patterns and numbers and relative numbers of introduced or cryptogenic species for all taxonomic groups.

<table>
<thead>
<tr>
<th>Taxonomic Group</th>
<th>Ascidiacea</th>
<th>Hydrozoa</th>
<th>Boring Bivalvia</th>
<th>Epifaunal Bivalvia</th>
<th>Infaunal Bivalvia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total # of species</td>
<td>184</td>
<td>397</td>
<td>25</td>
<td>149</td>
<td>299</td>
</tr>
<tr>
<td>Disjunct amphi-Atlantic</td>
<td>16 (8.7%)</td>
<td>68 (17.1%)</td>
<td>12 (48.0%)</td>
<td>11 (7.4%)</td>
<td>10 (3.3%)</td>
</tr>
<tr>
<td>Introduced</td>
<td>8 (4.3%)</td>
<td>7 (1.8%)</td>
<td>1 (4%)</td>
<td>2 (1.3%)</td>
<td>4 (1.3%)</td>
</tr>
<tr>
<td>Cryptogenic</td>
<td>3 (1.6%)</td>
<td>27 (6.8%)</td>
<td>6 (24%)</td>
<td>2 (1.3%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>Introduced + Cryptogenic</td>
<td>11 (5.9%)</td>
<td>34 (8.6%)</td>
<td>7 (28%)</td>
<td>4 (2.6%)</td>
<td>4 (1.3%)</td>
</tr>
</tbody>
</table>

The cryptogenic ascidian *Molgula manhattensis*

In Chapter 5 the history of a cryptogenic species was investigated using molecular tools. The ascidian *Molgula manhattensis* is one of the species with a disjunct amphi-Atlantic distribution (Chapter 4); its disjunct distribution pattern cannot be explained by larval dispersal or rafting. Furthermore, *M. manhattensis* has a recent history of introductions (in Australia, Japan, Russia, the Mediterranean and Black Seas, and the Pacific coast of the USA). The possible vectors responsible for these introductions were oyster transports and hull fouling, *M. manhattensis* is a common fouling species on American oysters (*C. virginica*) and ship hulls. Like other sea-squirts, *M. manhattensis* is a poor natural disperser, larvae are very short-lived and the adults are sessile and are not known to raft. The disjunct distribution pattern in the North Atlantic Ocean can therefore not be explained by natural long-distance dispersal mechanisms. In order to
investigate whether the European and North American populations of *M. manhattensis* are both relicts of the Last Glacial Maximum (LGM), we analyzed variation in the mtDNA COI subregion and reconstructed *M. manhattensis*’s phylogeographic history by comparing haplotypes in samples from both coasts of the North Atlantic, as well as samples collected from known introductions in other parts of the world.

The comparison of haplotype diversity across the Atlantic shows a nearly three-fold higher diversity on the Northeast American side as compared with the European side. The Northeast American populations showed a latitudinal diversity gradient, which is consistent with recolonization after the LGM from a southern refugium, and possibly also a northern refugium. *M. manhattensis* probably survived the LGM in the Northwest Atlantic with its natural substrate, the American oyster. Oddly, although *M. manhattensis* is very common on American oysters, it has not been recorded from shells of the European oyster *Ostrea edulis* or the Pacific oyster *C. gigas*. European populations did not show a latitudinal diversity gradient, but all samples were consistently low in haplotype diversity.

In the introduced range, two patterns were found. In Japan and the Black Sea diversity was low, which is in accordance with the classical view of introduced populations. However, San Francisco Bay haplotype diversity levels were comparable to those on the Northeast American coast. This is probably due to high propagule pressure. The vector of introduction into San Francisco Bay was the transfer of millions of oysters, and single oysters may introduce a number of individuals of *Molgula*. In contrast, the populations in the Black Sea and Japan were most likely introduced as hull fouling, which typically involves fewer individuals in an introduction event, and may result in low-diversity introduced populations.

Private haplotypes, which are an indication for long-term residence (i.e. preceding the LGM) of a species, occurred in all regions, except Japan. The presence of private haplotypes in introduced populations was unexpected, but may be explained by undersampling of northeast American populations (where these introduced populations originated), and high propagule pressure.

*M. manhattensis* is clearly native on the northwest Atlantic coast. However, distinguishing between an anthropogenic introduction and post-glacial recolonization in European waters requires multiple lines of evidence. Empirical evidence based on life-history traits, preferred habitat and a patchy European distribution (*M. manhattensis* being mostly restricted to harbors and marinas) argue for an introduction of *M. manhattensis* from North America to Europe. If it was introduced to Europe, the vector of introduction would have been hull fouling, as the first records of *M. manhattensis* in Europe precede the first American oyster transfers to Europe, which took place in the 1870s (Carlton & Mann 1996; Wolff & Reise 2002). For most invertebrates, the European coast is more diverse in the number of species than the North American coast. Post-glacial recolonization of the North American coast occurred from Northwest Atlantic refugia, and from refugia in Europe via Iceland (Wares & Cunningham 2001; Vermeij 2005; Maggs *et al.* 2008). Dispersal and recolonization in the other direction has not been documented, nor are there examples of species that are demonstrated to have a
naturally disjunct amphi-Atlantic distribution (Chapter 4). Taken together, these arguments support an anthropogenic origin of *M. manhattensis* in Europe.

The genetic data, however, present some challenges to the life-history and distributional data. Low haplotype diversity could also be the result of the LGM and does not necessarily mean that the European populations were introduced. The haplotype network showed the presence of nested, high frequency putative American haplotypes in introduced populations, but these were absent from Europe, which is unexpected given that there would have been a high chance of their presence had European populations been introduced, suggesting native residence in Europe.

Resolving the question rests on two inter-related factors: the degree to which the total haplotype diversity was sampled; and the relative role of vectors and propagule pressure at a given location. More intensive sampling of the Northwest Atlantic would certainly reveal more low frequency haplotypes, which could include the putative private haplotypes found in Europe. More intensive sampling in Europe might reveal additional private haplotypes and possibly the missing medium-to-high frequency American haplotypes, though the latter is much less likely. If European populations had been introduced, the vector would have been hull fouling, which is a vector with low propagule pressure when compared to oyster transports (Chapter 3). This could explain the low diversity of European populations. While more intensive sampling of the Northwest Atlantic might help to resolve some of the issues around low-frequency private haplotypes, it would not explain the absence of the higher frequency haplotypes in Europe. Thus, in conclusion, we cannot say with certainty that *M. manhattensis* was introduced to Europe, and it remains a cryptogenic species in Atlantic Europe.

**Conclusions**

The aim of this thesis was to determine to which extent natural patterns of diversity and natural distributions have been affected by anthropogenic species introductions. This question has been approached from different points of view, with different techniques and on different scales and levels of diversity.

The checklist of introduced species in the North Sea and the analysis of oyster associated introductions showed that the number of non-indigenous species is increasing. In fact, the North Sea is one of the most invaded seas in the world, with a high percentage of potentially harmful non-indigenous species (64%, Molnar *et al.* 2008). The most important vectors for species introductions in this region are hull fouling and shellfish translocations. Although the invasion process is highly unpredictable, and there are many examples of invasions with negative ecological and economic impact, oyster translocations are still taking place within European waters. Moreover, oysters are not the only commercial bivalves that are imported and relaid as is shown for the Oosterschelde estuary in The Netherlands. *Mytilus edulis* seed is imported from other European countries for restocking Dutch mussel culture, and despite a risk analysis
(Wijsman & De Mesel 2009), at least two non-indigenous species, the Atlantic oyster drill *Urosalpinx cinerea* and the Manila clam *Ruditapes philippinarum*, have recently been introduced by mussel imports from the United Kingdom and Ireland (Faasse & Ligthart 2008; 2009). Since established introduced species in marine environments usually are almost impossible to eradicate, management efforts of introductions in the sea should aim at preventing invasions by management of vectors (e.g. by banning shellfish translocations), rather than at reducing the impact of established invasions.

Determining propagule pressure for a single vector may aid in these management efforts. Detailed knowledge of vector characteristics, in particular propagule pressure, has been shown to be essential in explaining patterns of diversity. High propagule pressure explained the high diversity in introduced *M. manhattensis* populations, and the analysis of oyster-associated introductions and the epiflora of oyster shells revealed that even small numbers of imported oysters can result in large numbers of associated introductions. This process was further facilitated by the establishment of the vector itself, the non-indigenous oyster *C. gigas*, in receiving waters, which serves as a substrate for an increasing number of non-indigenous species.

Although most invasions have not been studied, and many of those that have been studied have shown that invasions fundamentally alter community structure and functioning, the intentional introduction of non-indigenous species as a biodiversity conservation method is again being considered (e.g. Briggs 2008). Assisted colonization is highly debated, as we do not know enough about the potential impact of non-indigenous species introductions to do a thorough risk assessment and predict the possible outcome of such intentional introductions (Ricciardi & Simberloff 2009). Assisted colonization and invasive species are two of the fifteen most important issues that were identified to potentially affect the conservation of biological diversity in coming years (Sutherland *et al.* 2010).

By estimating the scale of cryptogenesis, it has been demonstrated that the number of invasions is indeed highly underestimated. After analyzing distributions, natural and anthropogenic dispersal potential of individual species in detail, many of the species that we consider native should in fact be labeled as cryptogenic species, until their status is cleared up by thorough multidisciplinary studies that include molecular data. However, the phylogeography of *M. manhattensis* shows that it is not always easy to get conclusive results using molecular techniques. Although we did show that undersampling may have been an explanation for some of the discrepancies found in this study, other studies, based on fewer individuals and populations sampled, draw conclusions that are much more far-reaching, and the possibility of anthropogenic dispersal is rarely considered. This has great consequences for our understanding of the rate of evolution in the sea, as undoubtedly introduced species are included in some of these studies which are assumed to be native. Genetic diversity patterns within species caused by anthropogenic dispersal and by natural causes (such as the effects of the LGM) can be strikingly similar.

One question remains to be answered: **What is natural?** When studying marine communities, we should not by default assume that those species that are present in
our coastal waters are native and we should accept the possibility that many of these have been introduced in the past. Only those species that are proven to be native have natural distributions. Marine bioinvasions have been altering biological communities for centuries, and will continue to do so in the future. Completely natural ecosystems do not exist along North Atlantic coasts.