Arne Jernelöv

The Long-Term Fate of Invasive Species

Aliens Forever or Integrated Immigrants with Time?

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Preface

Alien, in the context of invasive species, means that the species, subspecies, or group with some specific genetic traits has (recently) been introduced by humans to a region, usually a continent or island, to which it didn't spontaneously spread. Mostly, alien is seen as a prerequisite for invasive.

The term invasive, when it is applied to a species other than human, is used with several different meanings. In the broadest understanding of the term, it means a species that, with the help of humans, establishes itself in an area outside its native range. In a somewhat more narrow understanding, it should not only survive for generations in the new territory but also undergo a drastic population expansion. A further limitation of the term comes when a damage criterion is introduced, mostly expressed in economic terms. Thus, the most widely used, human-centered definition reads "An invasive species is a plant or animal that is not native to a specific location; and has a tendency to spread, which is believed to cause damage to the environment, human economy and/or human health." In practice, as national governments and authorities are key players, the word "native" is understood to mean "from our country." Thus, the house finch, native to California and brought by humans to the US east coast, from where it has spread all over the USA, Mexico, and southern Canada and now numbers over a billion, is not classified as alien or invasive in the USA and Mexico. However, the house sparrow, with much lower numbers, but coming from Europe, is classified as invasive. Whether the house finch shall be seen as an invasive alien in Canada becomes a different administrative and philosophic question, since the original west coast population lately has spread north on its own and entered British Columbia, while the human-moved eastern population has spread to Ontario, Quebec, and the Atlantic provinces. Another example of a species that has been moved by humans within a country and then spread itself from the new location to other countries is the raccoon dog (*Nyctereutes procyonoides*). It was brought by humans from eastern Siberia to European Russia and Ukraine during Soviet times and then spread naturally from there to the Baltic states, Finland, and Sweden. It is regarded as alien and invasive in the latter countries, but not in European Russia.

Sometimes, a moral argument comes up for forgiving the invasiveness of a species when it prospers in an area to which humans brought it—when humans altered its native area to the point where the species can no longer survive there. The snowdrop (*Galanthus nivalis*) is about to become such a species thriving well on the British Isles and in Scandinavia, to where humans brought it, but fighting for survival in its native Continental Europe. Global warming is likely to produce quite a few such species. Are they to be seen as aliens that should be exterminated if possible, or are they refugees from our manipulations of the environment that we are morally obliged to give a new home in the world we altered?

In the definition of invasive cited above, the expression "is believed to" is used instead of the much stricter "has been showed to" or even more so "has been proven to." This can possibly be seen as an off-shoot of the wordings used in the definition of the precautionary principle from the 1992 Rio Summit, where it is said that "Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason to postponing cost-effective measures to prevent environmental degradation."

There is, however, a clear further weakening of the requirement to demonstrate damage, if "lack of full scientific certainty" is seen as the mother of "is believed to" and the question of who is authorized to be the believer immediately comes to mind.

Another aspect, if the precautionary principle is invoked, is the wording "cost-effective measures to prevent environmental degradation." This would seem to imply that measures to reduce or eradicate invasive species should only be undertaken if the cost of those measures is lower than the damage caused by the invader. (The methods used to calculate economic and ecological damage will be commented on in the concluding chapter.)

In this book, the term invasive is used without any damage criteria. I have used the term for species, which conquered new territories after having been introduced by humans, and that increased dramatically in numbers there. There are many of those, so to arrive at the 18 cases presented here, further selection criteria have been applied. First and foremost among those is time since introduction, as the long-term fate is the theme of the book. The order of the chapters with case studies also reflects this as they are presented following the year of introduction with the oldest, the earthworms, first.

The idea has also been to select examples from different groups of animals and plants, and organisms coming from and invading different geographical areas. The result comprises 18 cases: two parasitic fungi, three plants, six invertebrates (out of which three are insects), one amphibian, two birds, and four mammalians. Invaded areas are Africa, Asia, Australia, Europe, North America, Pacific Islands, and South America. The invaders come from Africa, Asia, Europe, North America, and South America. The invaded areas include terrestrial systems, as well as fresh and marine waters, in temperate and tropical areas in the northern and southern hemispheres.

Jarpas, Sweden Arne Jernelöv

Acknowledgments

The chapters in this book contain some seven hundred references, about 15% of the total number of publications I reviewed in the writing process. Most of them come from easily available scientific publications, but quite a few were found in much more difficult to access places such as 150-year-old articles in local small-towns, long-since-closed newspapers, in-house publications at various laboratories and institutes (so-called gray literature), articles in less common languages, or social network media postings. To retrieve it all has been a most challenging librarian task, and without the unwavering support of Michaela Rossini and her colleague Natalia Ovtchinnikova at the library of the International Institute for Applied Systems Analysis (IIASA), it would not have been possible for me to write this book.

I'm also indebted to Muki Jernelöv, my wife, for putting a lighter, native-speaker touch to the language and for editing the manuscript.

In addition, Bo Söderström, editor of *Ambio*, the environmental journal of the Royal Swedish Academy of Sciences, provided early inspiration for the book through our discussions about the fate of sparrows and finks in North America.

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Earthworms in North America

After the latest ice ages, earthworms were, by and large, absent from North America. Only in some sheltered regions that did not experience deep permafrost did the native species survive. It is a little known and seldom acknowledged and considered fact, however, that these earthworms didn't spread far after the glaciations. Thus, the prevailing earthworms found practically everywhere in North America and generally seen as natural, desirable, and self-evident components of the terrestrial fauna were more or less unintentionally brought in by European immigrants to become very successful invaders.

The Earthworms in Their Native Habitats

Earthworms are tube-shaped, segmented organisms that live in soil and feed on organic matter. They are invertebrates and thus lack a skeleton, but possess liquid-filled chambers which act as a hydraulic skeleton that can provide stability to whichever part of the body needs it at a given moment. They are very flexible, with longitudinal as well as transversal muscles. The digestive channel goes through the full length of the animal, and they are hermaphrodites, so each individual has both female and male sex organs. When mating, they reciprocally fertilize each other. Their coloration is mostly in the range of red-violet to gray-blue. There are globally some 2000 species of earthworms. In Europe, one of the most important groups is Lumbricidae, to which the common earthworm, *Lumbricus terrestris*, belongs. It can reach a length of 30 cm, which isn't much compared to the largest species, the 7 m long South African gigantic earthworm.

The workings of earthworms in the terrestrial ecosystem are well known. They live in the boundary layer between plant material such as decomposing leaves and grass on the surface and the mineral soil beneath. They live off of organic matter and act to speed up its decomposition by mixing more persistent parts of it such as humus with the inorganic soil components deeper down. In the process, the tunnels

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they dig facilitate aeration and drainage of the soil, which in turn further enhance microbial activity and release of nutrients.

Earthworms are generally well regarded in Europe and Asia, among farmers as well as scientists. Charles Darwin [1], who published a book about them in 1881, put great emphasis on their importance. “It may be doubted,” he wrote, “if there are any other animals which have played such an important part in the history of the world as these lowly organized creatures.”

One hundred and thirty years later, BBC Nature sang their praise: “Earthworms are the world’s unsung heroes. They loosen and mix up the soil, break down and recycle decaying plant matter and fertilize the soil by bringing nutrients closer to the surface. Birds often rely upon worms as a primary source of food.”

The common earthworm *Lumbricus terrestris*

As education for children, Skansen, an open-air museum and zoo in Stockholm, Sweden, writes on its home page: “Earthworms are small but very good farmers. They mix the soil and drag dead leaves down into the ground. Their tunnels go deep down and through them air and water can reach the roots of plants. They benefit other animals and plants.”

Introduction and Spread

Although hardly any records exist, it is obvious that earthworms of many different species were introduced to North America on many different occasions and to many different places. It is also very easy to imagine how it happened. Settlers from Europe often brought all sorts of plants with them from their home countries and with them soil around the roots. In the soil, there would have been earthworms.

However, one person is first and foremost seen as the one who happened to introduce earthworms to the New World. That person was John Rolfe. His place in the history of European settlement of America is secure also for several other reasons, even if it could be argued that his introduction of the earthworm was the action with the most far-reaching and long-term consequences.

John Rolfe was a settler in Jamestown, Virginia, the first successful English colony in North America, and he was the person that more than any other made it so. He married Pocahontas, the daughter of the local Indian chief, Powhatan, thereby securing peace and food assistance that were vital for the survival of the settlers. He also introduced and started the cultivation of the tobacco plant *Nicotiana tabacum*. When he returned to England in 1616, he brought with him not only his Indian wife but also a large cargo of tobacco from his farm at Jamestown. Both were a huge success in London. John Rolfe and Jamestown became rich from the regular shipments of tobacco to England, and the small colony became a boomtown with a rapidly growing population. The ships that came to fetch the "brown gold" carried ballast of stone, gravel, and dirt, which was dumped onto the beach to make room for the bales of dried tobacco leaves. With the ballast came the earthworms—or so the story goes.

It is well documented that the settlers in Jamestown during the first decade found it hard to grow any of the plants they brought with them. Historians have attempted to explain this and mostly looked for socioeconomic explanations, one of them being that few of the settlers had been farmers back in England. That might well have been a factor, as was in all likelihood the severe drought of the summer of 1609, but these circumstances may not be the whole explanation. Whatever the reasons, the consequences were dramatic. During the "winter of starvation" 1609–1610, 440 out of the original 600 settlers died. Survivors were abandoning the colony, when a ship carrying new immigrants, among them John Rolfe, arrived with provisions and seeds. But also in subsequent years, harvests were minimal, not only of grain but also of cabbage, turnips, and other vegetables. The only crop the settlers planted that grew well from the start was tobacco. They could trade and get maize from the Indians, but for the settlers, it seems they didn't really attempt to grow it for themselves. Eventually, little by little, their vegetable gardens finally started to produce.

Let's return to the reasons for the settlers' failure to produce adequate food. If the low crop yield in 1609 was really due to drought, why did they continue to be unsuccessful in the following years that enjoyed normal precipitation? If it was lack of farming skills, why did they immediately succeed with tobacco? One possible explanation is that tobacco and the maize that the Indians grew are American plants, the domestication of which had taken place in the absence of earthworms. The crops the Jamestown's settlers planted that failed to thrive were introduced from Europe and Asia, where earthworms have long had a decisive influence over the structure and quality of soils.

Back in Jamestown, earthworms slowly spread and started to give the soils in and around the colony a more European-like structure, which facilitated Eurasian plants to establish themselves there. This was, of course, the case not only for agricultural plants.

In a pattern resembling that of the highly suspect ballast in Jamestown, other, later, settlers came with plants and soil containing earthworms from their home countries. These became established and spread, in the slow way of worms, from their respective places of release. As a rule of thumb, earthworms on their own can extend their territory with a radius of maybe 10 m a year; so for their further spread inside North America, humans also played a key role. Besides gardeners, many of whom wanted earthworms to improve their soil and actively sought them out much of the spread was unintentional via transported plants and soil. Fishermen also played an important role, as can be concluded from the prevalence of earthworms around angling lakes and rivers. Leftover worms were simply released at the fishing sites. This resulted in that earthworms are now present in most North American habitats suitable for them. The different species, however, have a very uneven distribution, which has more to do with their haphazard pattern of introduction than their individual competiveness vis-à-vis each other in a given environment. One can conclude that as a group, earthworms have more or less conquered the continent, but the individual species have not yet reached their final distribution and, often enough, not yet met each other as competitors.

Notwithstanding the foregoing, to say that North America completely lacked earthworms after the latest glaciations is not quite correct. A not-so-small number of species, including a couple in the family Lumbricidae, did survive, but with a fairly limited geographic distribution outside the ice-free zones where they had hung on. With regard to the number of species of earthworms, the newcomers make up about a third, but with regard to number of individuals or biomass, they totally dominate.

Ecological Effects

The ground in a forest or meadow without earthworms is characterized by a layer of leaves and/or dead grass, often several decimeters and occasionally up to half a meter thick, representing several years of litterfall. Below this, there is mostly a thin

The ground in a forest where maple trees dominate and earthworms are absent. The leaf layer has been flattened after several months of snow cover. The leaves stick together, and the ones on the surface have been bleached, which indicates that no worms crawl through and disrupt it (Photo: G. Schlaghamensky and Kalev Jogiste [2])

A 20 cm long soil profile with a thick leaf layer to the right, fragmented leaves (the brown layer with light spots), followed by a layer of humus (black), and the beige mineral layer. The soil sampler is placed on the ground in question (Photo: G. Schlaghamensky)

layer of nutrient-rich compost soil and, underneath that, a clay or other mineral soil poor in nutrients [2].

Where earthworms are present, the previous year's litter generally disappears before autumn brings down another load. Under the thin layer of not-yet-degraded

The earthworms (*Lumbricus terrestris*, *L. rubellus*, and *Aporrectodea* sp.) have arrived and started to change the soil profile. A thin layer of leaves on the surface covers an even thinner, almost invisible, strata of leaf fragments below which the black humus has started to mix with the beige mineral soil (Photo: G. Schlaghamensky)

Here, the earthworms have changed the soil profile completely. The top layer no longer consists of leaves, as the worms quickly consume them, but of leaf fragments and twigs. Under this the soil layers are totally mixed, as they had been plowed (Photo: G. Schlaghamensky)

organic matter, there is a mixing zone of humus and mineral soil, on top of the clay or sand that lies beneath.

Earthworms transformed the soil of North American forests and grasslands with significant consequences for the viability and competiveness of many plants. With a thick layer of leaves and grass on the ground, budding plants must send out long roots to reach the moist and nutrient-rich humus, which, though rich in nutrients, it is only a thin layer. In the earth below, the concentrations of essential nutrients such as phosphorus and nitrogen are low. To succeed, the plants thus need to concentrate their nutrient-sucking root treads in this soil layer. For bigger plants such as trees, however, roots also have another essential function, which is to anchor and stabilize. To achieve this in a thin soil layer near the surface, the root system must be very dispersed and far-flung. A typical case is the redwood tree (*Sequoia sempervirens*). Deep roots would anchor the tree but be of little use for nutrient and water uptake. Native North American plants are generally adapted to this type of soil that used to dominate the continent.

In the thick, multiyear layer of leaves and grass lives a rich fauna of organisms. Insects such as millipedes, wood lice, springtails, mites, and spiders often dominate, but lizards, snakes, frogs, salamanders, mice, and shrews are also abundant. When the special environment that provides them with both food and protection shrinks in both time and area, the populations of these species often decline drastically [3–6].

Often, the earthworm densities are highest in the first years after invasion, when a large accumulated food supply is at hand. Later, densities adjust to type and quantity of recurring litterfall.

In cases where native North American earthworms co-occur with alien species and likely face some degree of competition, some reports suggest that the invader together with land-use change and habitat fragmentation had a strong negative impact on the native species [7], while many others found no such detrimental interaction between native and alien earthworms [4, 8].

Interacting Alien Species

While the Eurasian plants are evolutionary adjusted to the types of soils that earthworms create and maintain, their North American counterparts are not. When the structure of soil is altered, the competiveness of native species decreases, and the spread of vegetation from other continents with similar climate is facilitated [9].

That earthworms facilitate the establishment of Eurasian plant species by altering the structure of the soils can be seen as an established fact. To what extent this also means that they are important accomplices for the invasive success of, e.g., Japanese knotweed (*Fallopia japonica*), cheat grass (*Bromus tectorum*), and kudzu (*Pueraria montana*) in the USA, is less clear. In some cases, invading plants seem to return the favors and promote earthworms in return. For instance, biomass and abundance of invasive earthworms increased in plots dominated by European buckthorn (*Rhamnus cathartica*) probably as the low C/N ratio in their leaf liver is favorable for the worms (Heneghan and Steffen, unpublished) [5].

This general argument about invasive species facilitating for compatriots can be extended to the competitiveness of non-plant species as well. For example, introduced European birds such as starlings have earthworms high on their list of preferred food items and have evolved skills to locate and catch them, which the North American species had no general use for until the worms appeared.

Although this general reasoning makes sense (at least to me), it should be pointed out that I've found no specific scientific studies supporting or refuting the hypothesis of positive interaction of earthworms with other alien species than plants.

A study of the European earthworm *Lumbricus rubellus* and the Asian *Amynthas agrestis* in Tennessean soil found that a higher degree of food flexibility gave the Asian invader the upper hand in the competition with the European one [10]. On the other hand, a study of competition between the European earthworm, *Lumbricus rubellus*, and the Asian *Amynthas hilgendorfi* found no negative effect of the presence of one species on the other [11].

Economic and Human Health Impacts

An overwhelming part of all articles dealing with earthworms in North America describes them in similar positive terms as corresponding articles in Europe and Asia do there. The number of earthworms per surface area is often seen as a direct measure of agricultural soil fertility [12–15] and promoters of "organic farming" almost always stress that with their methods of cultivation, the number of earthworms will increase significantly. These in turn will not only help fertilize the soil, they argue, but also increase soil porosity so that more water can be stored, decreasing runoff and the risk of floods [16].

A very extensive review of the literature on the role of earthworms in soil formation and provision of ecosystem services, with 252 references [17] gave in the end a very positive picture of the contribution of these "lowly creatures," as Darwin termed them. However, in several studies included in the review, the positive picture was less clear, and in a few cases, the opposite conclusion was actually drawn.

Several attempts have been made to calculate the value of the ecosystem services provided by earthworms in economic terms. An early and often cited study [18] arrived at a global figure of US$75 billion a year for soil improvements. If one approximates this figure in relation to North America's share of global land under cultivation, about 15%, one comes to an annual value of US$11.25 billion.

Another approach to the question was used by the professors Steve Wratten and Ross Cullen at Lincoln University, New Zealand [19]. Their calculations were based on the value of fertile topsoil and the amount of such that earthworms produce in a year. The result would then be proportionate to the density of worms in the soil. Their standard example was 1.3 tons of earthworms per ha, which gave a value of US$54 per year. Recalculated to North American prices and size of land under agriculture (4.7 million km^2) and using the same earthworm density, the figure would be $12 billion annually.

This, however, is far from the whole picture. During the last decade, forest scientists in particular have started to describe earthworms in negative terms [20]. One part of their argument has been, contrary to many other studies some of which are referred to above, that the accelerated degradation of organic matter caused by the earthworms leads to an increased loss of nutrients. Their most important argument, however, is that the increased difficulties for native plants, foremost trees, to root themselves in the soil that earthworms create—a claim about which there is full consensus—have not only ecological but also economic repercussions [21].

As this article also highlights, it is not only European earthworms that have invaded North America but also Asian ones, in particular the *Amynthas* species, which arrived late in the nineteenth century. Some vocal scientists see them as an even worse threat than their European counterparts to the remaining natural forests in North America.

In summary, though, the positive economic effects on North American agriculture and horticulture are so strong that it's highly unlikely that the effects on forestry, when they in the future get assessed, can change the picture of an invasion with a clear black bottom line.

There are some articles that speculate about the possibility that earthworms may carry certain bacteria and viruses that could be detrimental to human health and thereby spread diseases, but there are no actual case studies to substantiate the claim, besides reports of diarrhea after consumption of mouthfuls of earthworms.

Control Efforts

There have been no reported serious attempts to eradicate earthworms once they got established. There's some information given to anglers in particular, arguing that they should not dump leftover bait worms in still earthworm-free areas. Generally, though, much more efforts are spend actively spreading them than preventing their spread.

Current Status and Likely Future

Although earthworms today are spread over most of North America except for the far north, mountain areas, and deserts, where they can't live, and some forest areas they have not yet reached, the different species still mostly occur in a distribution pattern reflecting the haphazard nature of hundred thousand introductions to new sites.

With time, counted in centuries, different species, invasive and native, will coexist in the same areas and subdivide it into ecological niches. Their collective impact on soil will be even stronger, when the different species do what they are best at. In this context, it's worth pointing out that the same human-caused distribution factors that spread the invasive species are at work on the native ones and that they also transform the soil, when they enter an earlier earthworm-free area. The domination of the newcomers is however likely to continue.

Public Perception and Current Policies

The public perception of earthworms in North America is overwhelmingly positive. They are seen as indicative of fertile and healthy soil. Forest ecologists' recent concern has not (yet) had much impact either on the public at large or on decision makers. Thus, there are no specific anti-earthworm policies in place or under preparation [22].

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Zebra Mussels in Western Europe and North America

Cautionary Tale

In a cautionary tale from the nineteenth-century Holland, a poor lockkeeper was faced with additional hardship when masses of mussels suddenly colonized the locks and prevented their operation. Removal of the mussels required hard work and was very time-consuming, and he suffered numerous, easily infected cuts. The poor man had to hire a helper, whom he could barely afford to feed. His luck changed, though, when he discovered that the chickens on his tiny farm, adjoining the locks, eagerly ate the small mollusks and that he, with an unlimited source of free food for them, could thus raise them in large numbers. In the end, he became a wealthy egg producer.

The story is told as one of a blessing in disguise, but there is far from being a consensus that zebra mussels qualify as such.

The Mussel in Its Native Habitat

The **zebra mussel** (*Dreissena polymorpha*) is a small freshwater **mussel** originating in lakes and rivers in Southern Russia. The name zebra mussel derives from the stripes on its triangular shells, although this color pattern is not always prevalent. They are filter feeders and attach themselves to hard substrates with strong byssus threads emanating from their umbo on the hinged side. They often form large colonies with mussels attached to one other, much like *Mytilus* mussels in the marine environment. Densities measured in thousands per m^2 are common [1], but tens of thousands are not rare, and one study reported as many as $114{,}000/m^2$. The individual mussels are generally small, 1–2 cm in length, but they can grow up to 5 cm. Their biomass varies as a function of density, size, and condition and is mostly within the range of 0.2–20 kg/m^2. Their lifetime is relatively short, typically 3–8 years.

A. Jernelöv, *The Long-Term Fate of Invasive Species*,
DOI 10.1007/978-3-319-55396-2_2

Close-up of a typical shell of a zebra mussel (Photo from Wikipedia). http://en.wikipedia.org/wiki/File:Dreissena_polymorpha3.jpg

Live zebra mussels underwater with shells open, animals respiring, and siphons visible (Photo from Wikipedia)

Dependent on the size of the mussel and water temperature, a zebra mussel will filtrate 1–5 L of water a day, consuming what it finds edible and depositing feces and nonfood particles covered in mucus, so-called pseudofeces, on the bottom. Sexual maturation of zebra mussels can occur early, and cases have been reported in which, before they have been settled for 2 months, they already release eggs and sperms [2]. Normally, however, they start doing that in the second year at a size of just under a centimeter.

An adult female can produce million eggs in a year and over five million in her lifetime. Veligers, the tiny, free-swimming larvae of the zebra mussel, will settle onto any hard surface within a week or two of birth. They have some tendency to swim against the current, but are largely carried along with it [3]. Other authors have made much lower estimates of the fecundity of the zebra mussel females, giving 150,000 eggs in a year as a high.

Small zebra mussels have a number of predators in their area of origin. Fish such as sturgeon, catfish, carp, and eel feed on them, as do many species of birds and crayfish.

Copepods such as *Cyclops* also feast on veligers.

The zebra mussel is a freshwater species but tolerates salinities up to 6 PSU (or per mile). Its natural habitat includes brackish water areas of the Caspian and Black Seas.

The Spread to Western Europe

In the eighteenth century, a number of canals were dug to connect Russian rivers going to the Caspian Sea with those emptying into the Black Sea. Later, the canal system was extended further westward and connected to those in Central and Western Europe. The canals and the rivers they connected became the first steps along the route of the zebra mussel's westward spread. They were found in Hungary and Slovakia in 1794 [4], only a quarter of a century after it was first described by Pallas from specimens collected in the Ural, Volga, and Dnieper Rivers. Grossinger, at the time he found the mussel in the Danube basin, did not think of it as an invasive species, but in Rotterdam, the Netherlands, it was very much seen as such when it appeared there in 1827, particularly when it started to interfere with the operation of sluices [5].

The concept of a more western native distribution range of the zebra mussel is, however, not without modern subscribers. The December 2014 issue of the journal *Water Technology* states that "They were originally found in the Balkans, Poland and the former Soviet Union" [6]. Most scholars, however, see the Caspian and Black Sea drainage areas as the native home of the zebra mussel and some only the former.

Already prior to its detection in the Netherlands, the zebra mussel had started its conquest of the British Isles, starting in Cambridgeshire in the early 1820s, reaching London in 1824, Yorkshire in 1831–1833, the Forth and Clyde Canals in 1833, and the Union Canal, near Edinburgh, in 1834 [7, 8].

Obviously, the zebra mussel is much more likely first to have reached England on board a ship rather than attached to the exterior of one, as their saltwater tolerance probably is not high enough for them to have survived the Channel crossing otherwise. Similarly, it is likely that the mussel had reached Lake Mälaren and Sweden with ballast water, or otherwise on board a ship, when it was first spotted there a 100 years later.

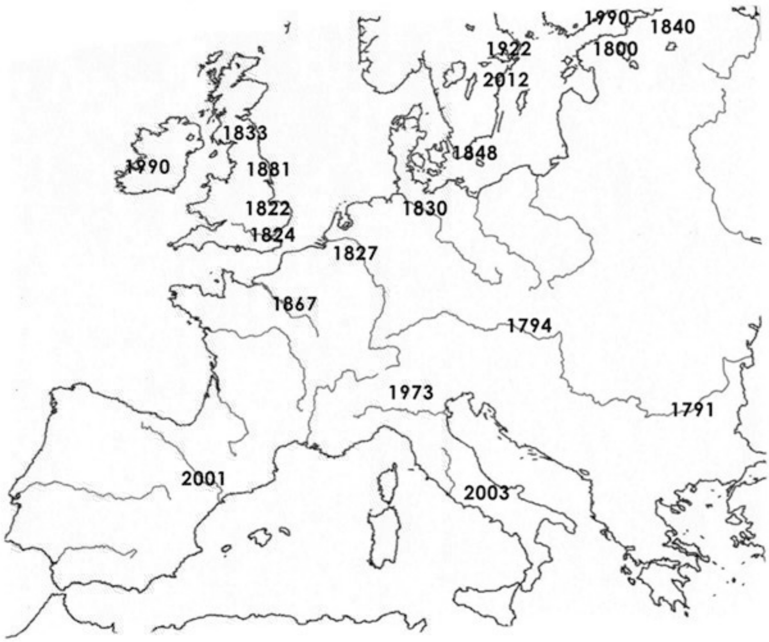
By that time, the zebra mussel had long since taken over the European canal system and was common over most of Germany and France. Hamburg had been reached already in 1830, Copenhagen in 1840 [9] and the river Seine outside of Paris in 1867.

To the Mediterranean parts of Europe, the zebra mussel arrived much later. In Italy, they first appeared in Lake Garda in the north in 1973 [10] and in Tuscany in the central part in 2003 [11, 12]. In Greece, they were first reported in the early 1980s [13].

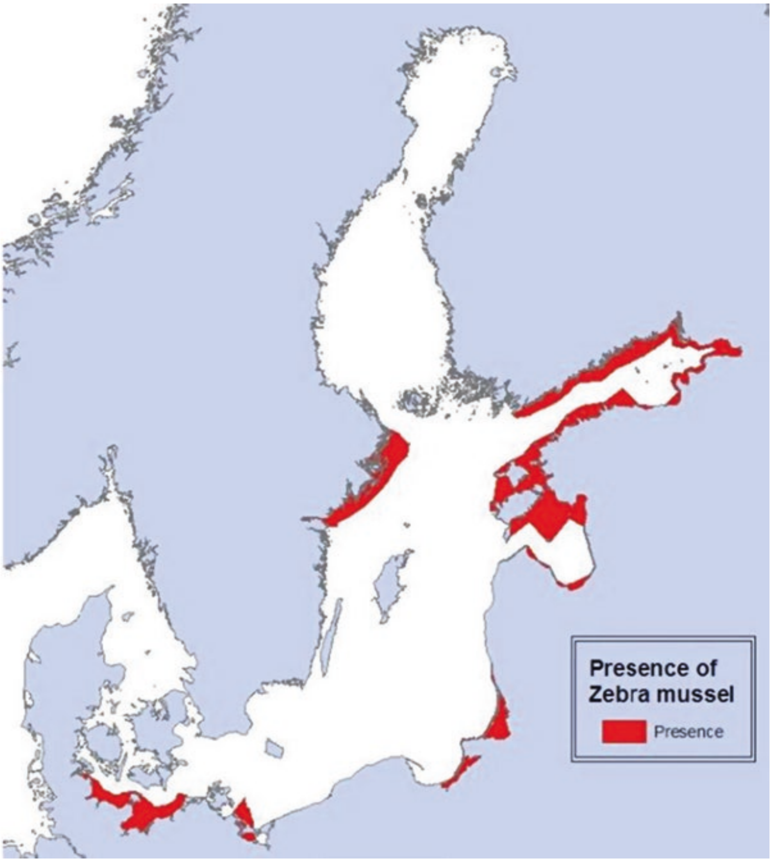
In Spain, the first populations were detected in 2001 in the Flix reservoir, from where they gradually spread until fully colonizing the Ebro basin. Four years later was found in the Sitjar reservoir on the river Mijares [14].

In the more remote areas of Northern Europe, the zebra mussel also arrived later. In the Shannon estuary in Ireland, they appeared in the 1990s, some 170 years after reaching England, and spread throughout the Shannon and Shannon-Erne catchments [15]. To Finnish territorial waters, the zebra mussel came in the 1990s, after having been present in the nearby large Russian Lake Ladoga for 150 years and in Estonia for a similarly long time [16, 17].

The invaded areas of Western Europe also include some other brackish parts of the Baltic, as well as estuaries in the North Sea and Irish Sea. Here, the densities are mostly much lower than in freshwater, and in competition with the *Mytilus* species, *Dreissena*, the zebra mussel loses out as soon as salinity is high enough to support those other marine organisms.



The spread of zebra mussels in Western Europe



The presence of *Dreissena polymorpha* in different coastal areas in the Baltic (source: HELCOM List of non-indigenous species). Note that the distribution in the Gulf of Riga and Swedish Baltic Proper is limited to more freshwater parts

Effects of the Zebra Mussel in Newly Invaded Waters in Western Europe

In West European freshwater systems, the zebra mussel represents a new type of organism due both to the high population densities in which it occurs in suitable habitats and to its filter-feeding mechanism, which relocates nutrients from the water mass to the bottom, thereby depleting the pelagic and enriching the benthic community. Clearer water also allows sunlight to penetrate deeper, thereby extending the reach of attached algae and rooted plants.

Native freshwater mussels in the genuses *Anodonta*, *Unio*, and *Margaritifera* have much lower population densities, live much longer, and reproduce more slowly and in a complicated fashion (the larvae during each stage are parasites of different fish species). Several of the species are rare and even threatened by extinction in many or most countries. They also live by filtering water, but have little effect on the nutrient relocation due to their smaller numbers and biomass. The invading zebra mussel affects these native mussel species negatively in two ways: They outcompete them for food, and they overgrow them, thereby hindering their movements, and may even bind them with their byssus threads to the point to which they cannot open or close their shells.

The effects of zebra mussels on phytoplankton communities and on particle deposition rates have been the subject of many studies, for example, on Russian canals and water reservoirs and Polish lakes. Generally, a much increased deposition rate, a substantial reduction of phytoplankton, and a more light penetration have been reported [1, 7].

A meta-study based on 47 underlying reports concluded that the introduction of *Dreissena* generally was associated with increased benthic macroinvertebrate density and taxonomic richness. The effects were positive on the densities of scrapers and predators, particularly leeches (*Hirudinea*), flatworms (*Turbellaria*), and mayflies (*Ephemeroptera*) and also had strong positive effects on gammarid amphipods. Gastropod densities also increased in the presence of *Dreissena*, but large-bodied snail taxa tended to decline, as did sphaeriid clams and other large filter feeders and burrowing amphipods (*Diporeia* spp.) [18].

In a study in the slightly brackish waters (1 PSU) of the western part of the Szczecin Lagoon in Poland, it was found that the fauna of macrozoobenthos, comprised primarily of oligochaetes and chironomids, increased with a factor of 2.4–4.9 near the zebra mussel beds when compared to more remote localities with similar sediment structures. Chironomids, oligochaetes, and *Gammarus* amphipods were particularly favored [19].

With regard to human technical installations in water, the zebra mussel has caused significant damage. In populating supply pipes, they reduce water flows. They damage boats, engines, fishing gear, buoys, locks, and docks and turn bathing beaches into foot- and hand-cutting underwater torture fields.

After Their Introduction, What Happened Next in Western Europe?

The typical picture, repeated many times over in Russia, continental Northern Europe, Britain, Sweden, and, more recently, in Ireland and Spain, is that once established in a water system, the zebra mussel will spread throughout it. This spread will be particularly fast where boat traffic is intensive, as it is in canal systems. In this initial phase, mussel densities will also be extremely high, but after some years, densities decrease and more or less stabilizes at much lower levels [1, 20, 21].

In this context, a special double interaction between zebra mussel and crayfish has been noted. On one hand, crayfish eat (small) mussels and reduce population densities [1, 22, 23].

On the other hand, zebra mussels settle on crayfish and may impair their mobility and feeding possibilities [24].

Studies in Polish lakes have shown that roach, with their strong pharyngeal denticles, adopt to feed almost exclusively (95–100%) on zebra mussels and that their predation impact may become significant [3, 25].

Crayfish covered with zebra mussels.

Photo jpeg mcarp

When zebra mussels are present in a water system, even as natural and human-induced mechanisms for further overland spread to nearby water systems of both veligers and adult mussels can easily be imagined, these mechanisms appear to be relatively ineffective. In Sweden, for instance, the zebra mussel was introduced to Lake Mälaren in the 1920s, but some 80 years passed before they were found to inhabit another freshwater system, the Göta Kanal, despite a low-level presence in the Baltic archipelago to which both systems are connected [26].

The European attitude to the zebra mussel is not all negative. Most of Europe's inland waters have been affected by eutrophication. Increased nutrient loads, most importantly of phosphorus, have led to increased phytoplankton densities, more turbid waters, anoxic bottoms, diversity losses among aquatic plants, and a shift in fish populations. Environmental measures since the 1970s have reduced but not eliminated these problems. The presence of zebra mussels in many ways counteracts the effects of eutrophication and in some respects restores water bodies to the status they had some 100–150 years ago, which also has a positive effect on shoreline property values. This has in turn led to proposals and experimental attempts to deploy the zebra mussel for restoration of overfertilized bodies of water.