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MARINE BIOLOGICAL INVASIONS

PHILIPPE GOULLETQUER

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INTRODUCTION
Are terrestrial invasive species getting all the media attention?

The introduction and spread of alien (or 'exotic') species, leading to biological invasions, is one of the major causes of biodiversity loss worldwide. These invasive alien species (IAS) can, in some cases, compete with local species, modify environmental conditions and the services provided by the environment (ecosystem services), or damage economic activities and human health. A study published in 2021 in the scientific journal *Global Change Ecology* showed that 14% and 40% of functional diversity (habitats and biomass) for mammals and birds, respectively, were threatened by biological invasions (Bellard *et al.*, 2021). For the European Union (EU) alone, the economic costs of such impacts are estimated at more than 138 billion euros (€bn) for the period 1960-2020, of which nearly €8bn is fully documented, with 10.28% allocated to management costs. Projections for 2040 suggest a further deterioration, with costs expected to reach at least €22 billion for the EU, including €2.4 billion for France (Henry *et al.*, 2023). This issue has therefore become a major concern for many land managers and for the development of public policies.

The issue is covered by all the international conventions dealing with environmental and development issues. The phenomenon is particularly serious in island systems, where the introduction of cats and rats, for example, is responsible for the extinction of endemic species. The disappearance of the dodo (*Raphus cucullatus*), an endemic bird of Mauritius, at the end of the 17th century is a case in point. Its extinction is the direct result of human activities, as it fell victim to hunting activities, changes to the soil caused by imported crops and the predation of eggs by various exotic species that were also imported (rats, dogs, cattle). Today, the kagu (*Rhynochetos jubatus*), a phylogenetically unique bird species emblematic of New Caledonia, is similarly threatened with extinction by rat predation. Moreover, these changes can also be documented on a continental scale. For example, the case of the multiple introductions of exotic earthworms into North America, whose initial biodiversity had declined sharply following the last ice age, is also exemplary. More than 97% of the North American continent has been colonised by 70 species of earthworm originating from Asia and Europe, representing a quarter of this biodiversity, which plays a major ecological role (Mathieu *et al.*, 2024).

For some ecosystems that are major contributors of food resources, voluntary introductions have proved catastrophic. In Africa, for example, the Nile perch (*Lates niloticus*), a powerful carnivore and very good swimmer, was introduced into Lake Victoria in 1954 to counter the collapse of the population of Victoria tilapia (*Oreochromis variabilis*) and Singida tilapia (*O. esculentus*), two species naturally present in the lake. Initially seen as the ‘saviour’ fish, contributing to the diet of more than 47 million people in the three neighbouring countries (Uganda, Tanzania and Kenya), this introduction has proved problematic for the environment, with the disappearance of more than 200 species of native fish and the disruption of the entire ecosystem. After peaking at almost 380,000 tonnes in 1990, landings have fallen to just under 200,000 tonnes since 2020. It should be noted that production is supplemented by the exploitation of another species introduced at the same time, the Nile tilapia (*O. niloticus*).

France is directly concerned by the problem, with numerous examples in both mainland France and the overseas territories, with more than 3,700 exotic species to date in France overall (there are 1,459 species on average per EU country) (Henry *et al.*, 2023). The French Biodiversity Agency (*Observatoire National de la Biodiversité*: ONB) indicator shows that an average of 12 IAS are introduced into a French *département* every decade, and that the rate is increasing. This threat is particularly acute in French overseas territories, where 74% of French IAS are concentrated, causing irreversible damage to local and endemic flora and fauna. Furthermore, 60% of the world’s 100 most invasive species have been identified in these overseas territories.

These include the *Miconia calvescens* tree, nicknamed the 'green cancer' of Tahiti, which is proliferating at great speed, to the detriment of the local flora. Introduced in 1937 as an ornamental plant, it now covers two-thirds of the island (Meyer, 2023).

Nowadays, the issue of biological invasions is appearing more and more in public debate and in major national and regional media, especially in connection with a few emblematic cases. The coypu (*Myocastor coypus*), American mink (*Neovison vison*) red-eared terrapin (*Trachemys scripta elegans*), common wall gecko (*Tarentola mauritanica*), — which arrived in the south of France in the early 1980s and has gradually colonised the entire coastline, replacing the common wall lizard (*Podarcis muralis*) —, bullfrog (*Lithobates catesbeianus*), ring-necked parakeet (*Psittacula krameri*), Japanese knotweed (*Reynoutria japonica*), water primrose (*Ludwigia sp.*), mimosa (*Acacia dealbata*), frogbit (*Limnobium laevigatum*), pampas grass (*Cortaderia selloana*), native to South America, pickeral weed (*Pontederia cordata*) and water hyacinth (*Eichhornia crassipes*) are all invasive species that threaten the environment, the economy and, in some cases, public health. Some threaten human health by carrying diseases, such as the tiger mosquito, which carries the dengue and chikungunya viruses, or by causing allergies, such as ragweed, which causes conjunctivitis, asthma and urticaria, or by being toxic to humans, such as giant hogweed (which causes burns). This problem affects the vast majority of plant and animal groups. Exotic plants such as the sour fig (*Carpobrotus edulis*), prickly pear *(Opuntia ficus-indica*) and century plant *(Agave americana)* have proliferated to such an extent that 200 tonnes of them had to be removed (at great expense) from the calanques of Marseille between 2017 and 2022 in order to protect astragalus *(Astragalus tragacantha*), an emblematic plant of the area. The number of projects to dig out exotic plants, involving the general public, is increasing in France. Sour fig, Himalayan balsam (*Impatiens glandulifera*) and Japanese knotweed were dug out in the Lannion-Trégor community (Côtes-d'Armor) in 2024 to preserve coastal biodiversity.

The most recent cases, which have also received a great deal of media coverage, include the Asian hornet (*Vespa velutina*), which was recently joined by the Oriental hornet *(Vespa orientalis*) in 2021 (Marseille, 2021), the virile crayfish (*Fraxionus virilis*) (Yonne, 2021), electric ant (*Wasmannia auropunctata*) (Toulon, 2022), and tiger mosquito (*Aedes albopictus*). American crayfish, particularly the Louisiana crayfish (*Procambarus clarkii*), are responsible for a wide range of damage, both to biodiversity (direct competition with many animal species) and to habitats, due in particular to their burrowing activity. In 2024, following heavy early-summer rains, the red swamp crayfish, a species introduced in the late 1970s for commercial purposes, invaded several areas of the Atlantic coast, spilling out onto roads, gardens, car parks, etc. Population densities were so high that the crayfish saturated available space and pushed into new territories. Hardy and voracious, this species, having already displaced other non-native crayfish, continues to expand exponentially through the country's freshwater systems, disrupting ecosystems by preying on amphibian eggs and young fish, and by digging burrows that erode riverbanks.

Although the problems are similar, biological invasions in the marine environment do not attract as much attention as those on land. In less accessible environments, ecosystem characteristics are less well studied, which makes marine IAS, primarily coastal macrofauna and macroflora larger than 1 mm, less visible. However, a few cases have been highlighted in order to inform the public about the threats that primarily affect either public health or human activities, especially fishing. The brown seaweed *Rugulopteryx okamurae*, which arrived in the 2000s and originated in Japan, is now present throughout the Parc des Calanques and in several Mediterranean areas. Here, it is transforming the habitat by completely covering the rocks, thereby creating a significant change in the marine flora and fauna (Ruitton *et al.*, 2021). This species also arrived in Gibraltar in 2015 and has colonised Spanish waters as far as the Canaries and the Basque Country, causing considerable damage to biodiversity and the fishing industry. As with 'green tides', its degradation forms a 'bank' of biomass and, as it rots, releases hydrogen sulphide, which is harmful to humans (García-Gómez *et al.*, 2021a).

The American blue crab (*Callinectes sapidus*) is also a species of great concern in the Mediterranean, both for the environment and for human activities. Some species of fish are also reported in the media because of their significant impact: the square-tailed rabbitfish (*Siganus luridus*) owes its name not to its appearance, but to its diet. It is a highly efficient herbivorous fish native to the Indian Ocean, capable of ravaging the seabed and profoundly altering its environment. The invasion of Caribbean waters by red or common lionfish (*Pterois volitans* or *P. miles*) has disrupted the entire ecosystem of the region, especially the structure of coral reefs. Similar impacts have been observed in the eastern Mediterranean since the arrival of *P. miles*. This species is of particular interest because of its expansion towards the western Mediterranean. For more insidious and invisible reasons, the proliferation of ostreopsis *(Ostreopsis ovata*), a microalga of tropical origin, is also attracting attention because it is responsible for toxins dispersed as aerosols via sea spray. These toxins can contaminate beach users by inhalation, causing symptoms that are often similar to flu. This microalga has already caused beach closures and hospitalisations in the Mediterranean and on the Basque coast in recent years. Alongside these few high-profile species, several hundred exotic species have been present on coasts of mainland France and French overseas territories for many decades, or even centuries, some having become part of our natural heritage, others being exploited. However, many have arrived on our coasts more recently (Goulletquer, 2016). Every year, new reports that could lead to new biological invasions are recorded, such as the red alga (*Lophocladia lallemandii*), identified in the Port-Cros national park in 2021. Several dozen species are either directly responsible for, or commonly associated with, significant impacts on the environment and/or human activities.

The aim of this book is to throw light on the process of marine biological introductions and invasions, specifying the vectors and pathways of introduction, the impacts caused, and the management methods implemented to meet this challenge. The contribution of all aspects of scientific research is essential here, in order to provide the most convincing results for managers and public decision-makers, who will be able to draw up new public policies and regulations at national, European and international level.

WHAT DO WE KNOW ABOUT BIOLOGICAL INVASIONS?

WHAT DO WE MEAN BY 'INVASIVE SPECIES'?

Although the terminology is not yet fully established, it is important to clarify the terms used in the field of biological invasions. (Soto *et al.*, 2024; Vilizzi *et al.*, 2025). This is a complex subject with a variety of semantics, due in particular to the different cultural perceptions of 'man-nature' relationships.

For example, there are various terms for introduced species, such as 'alien', 'exotic', 'non-native', 'non-indigenous', 'allochthonous' and 'xenobiotic', often used synonymously and sometimes depending on the context. They refer to species that have been intentionally or accidentally transported by human activity to a region where they were not originally naturally present (i.e. outside the species' historical native range). This implies a break in the species' natural range, for example a species naturally present and initially described in the Caribbean, its native range, being found and identified in the Mediterranean Sea.

Conversely, a change in the range of a species resulting, for example, from climate change, which is an increasingly frequent situation, does not correspond to an introduction, since there is no break in the distribution range. These are referred to as neo-native species (Essl *et al.*, 2019).

Similarly, it is necessary to avoid any parallels with issues of human immigration, as sometimes discussed in the social sciences, insofar as human population movements do not meet the criterion of a break in distribution area. *Homo sapiens* has been present for several millennia throughout the world, with the exception of there never having been perennial human populations in Antarctica (Rémy and Beck, 2008; Warren, 2021)!

Some species are described taxonomically, but their natural area of origin cannot be determined. These are known as cryptogenic species, whose origin is unknown (Carlton, 1996; Jaric *et al.*, 2019). A typical case would be the inventorying of previously undescribed species present in the biofouling on the hull of a merchant ship that had transited several continents before being refitted in a dry dock in a European port.

In a more complex way, certain groups of species that are not morphologically distinct may meet the definition of 'species' through reproductive isolation, or the phylogenetic definition of species (strong genetic differentiation of lineages due to ancient divergence). A complex of native and exotic species, known as 'cryptics', can thus be found, which justifies the widespread use of genomic approaches to characterisation beyond morphological criteria alone (Jaric *et al.*, 2019).

Some of these introduced (non-native/exotic/non-indigenous) species survive and establish natural populations, and a fraction of them may become invasive. The term 'invasive' applies to exotic/non-native species that spread, with or without human assistance, in natural or semi-natural habitats. These species induce a significant change in the composition, structure and functionality of ecosystems and/or cause significant economic losses and/or have effects on human well-being and public health and, ultimately, induce additional management costs. The term 'invasive' has a strong connotation of urgency, risk and negative impact. Some definitions, such as that of the United Nations Environment Programme (UNEP) in 1994, restrict the 'invasive' characteristic to species that have a negative impact on host ecosystems. However, this criterion of negative impact can be subjective and relative, because it is anthropocentric. Even if the vast majority of impacts are considered 'negative', it is necessary to consider all the effects on biodiversity and on the ecosystem services produced, including both 'negative' and 'positive' (e.g. supply services) (Kourantidou *et al.*, 2022; Tsirintanis *et al.*, 2022). For example, the proliferation of the Manila clam (*Ruditapes philippinarum*) has had a 'positive' effect on the winter survival rates of marine avifauna on British coasts, through improved availability of prey (Caldow *et al.*, 2007).

The creation of habitats by so-called 'engineer' species can be 'positive' in certain respects, such as the increased availability of refuges for other local species, but 'negative' in others, considering the impact on the original natural habitat, or even by favouring the arrival of new exotic species (e.g. novel ecosystem) (Tsirintanis *et al.*, 2022).

As far as marine biological invasions are concerned, we will stay with the category of invasive non-native alien species (IAS) insofar as the management methods differ profoundly between native and non-native species. Green tides, for example, which have had a great deal of media coverage, are environmental problems linked to the eutrophication of environments. They call for upstream management measures at catchment basin level, whereas IAS are a matter of their own characteristics as they develop in a new environment. From the point of view of management methods and regulations, the issue is also very different. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008, known as the Marine Strategy Framework Directive (MSFD), identifies two distinct descriptors, No. 2 for 'non-indigenous species' (NIS) and No. 4 for 'eutrophication' in the case of green tides. Similarly, EU regulation 1143/2014 is dedicated solely to the «prevention and management of the introduction and spread of invasive alien species»[1].

A number of other terms are used to describe the different types of non-native species. Some non-native species may be observed from time to time ('occasional species'). These reports refer to taxa (species, subspecies, race, variety) introduced without the development of a perennial population. For example, the breeding of kuruma shrimp (*Penaeus japonicus*) during the summer in the maritime marshes of the French Atlantic coast has led to escapes and to reports of individuals in open environments, but no wild populations have appeared to date. This is also the case for the American blue crab on the same Atlantic coast, which has been occasionally observed following deballasting

1. https://eur-lex.europa.eu/legal-content/FR/TXT/PDF/?uri=CELEX:32014R1143

since the beginning of the 20th century (Goulletquer, 2016). What remains to be done is to analyse their future in the face of changes resulting from climate change!

Populations of 'established/acclimatised' taxa refer to the processes followed by a non-native species developing perennial populations following its introduction and successful reproduction. This is the initial stage that precedes 'naturalisation', when such a species becomes permanently established in its environment and integrated into the local ecosystem after several generations. Consequently, a naturalized species will be successful when it has overcome the following three barriers: geographical displacement, resistance to local environmental barriers and regular reproduction over time.

'Feral' populations refer to organisms, or their descendants, derived from escapes and having developed perennial populations after reproduction. Several non-native species used in aquaculture during the 20th century have developed such wild populations on the Atlantic coast: the hard clam (*Mercenaria mercenaria*), Manila clam, and Pacific oyster (*Magallana gigas*), formerly known as *Crassostrea gigas* (Goulletquer and Héral, 1997). Nowadays, these species are caught both professionally and recreationally. Wakame (*Undaria pinnatifida*), a macroalga native to Asia, was detected in Thau lagoon in 1971 and associated with the introduction of *M. gigas*. It was deliberately introduced into Brittany in 1983 for seaweed farming. After escaping from its cultivation area, this macroalga developed perennial populations on Brittany's coasts (Voisin *et al.*, 2007). Today, it is present on the coasts of Ireland, Scotland, the Netherlands and as far south as Spain as a result of seaweed farming activities and secondary introductions (Epstein and Smale, 2017). Escaped farmed individuals may also hybridise with wild populations, thereby altering their genetic characteristics, as observed in Atlantic salmon (*Salmo salar*) (Perriman *et al.*, 2022). Currently, these difficulties have led to a call for a halt to salmon farming in Canada in response to the 'endangered' status of wild, native populations of chum salmon (*Oncorhynchus keta*).

Another situation that needs to be clarified is 'translocation', which refers to the introduction of a species native to a geographical area within a country into another area of the same country where it is not native. The different coastlines of mainland France provide examples of this type. For example, the voluntary translocation of Mediterranean mussel spat (*Mytilus galloprovincialis*) to the Normandy coast for farming there was carried out in the 1990s. The case of the accidental introduction of *Tritia neritea*, a nassariid gastropod, is also a good example. A study of the genetic structure of this mollusc, whose native range extends from the Mediterranean to the Atlantic coast of Morocco and southern Spain, has shown translocations to the French Atlantic coast and the English Channel via movements of shellfish stocks since the 1970s. Since then, it has been competing with the local species, the netted dog whelk (*Nassarius reticulatus*) (Simon-Bouhet *et al.*, 2016; Boissin *et al.*, 2020). This situation is important in terms of management when we consider the official reference lists of IAS, but also of protected species. These lists are drawn up on a national scale by means of single lists, with no distinction being made between occurrences on the different coastlines. The issue is even more complex when a species is the subject of protection measures or has 'endangered' status in its native range.

HOW DOES A BIOLOGICAL INVASION TAKE PLACE?

Biological invasion should be seen as a process that enables a species to break through 'barriers'. The introduction of individuals or reproductive elements (eggs, propagules) enables an initial geographical barrier to be crossed via direct or indirect human-mediated vectors, going beyond the species' natural range (e.g. maritime transport, Suez Canal). Subsequent dispersal, known as 'secondary' dispersal, may be facilitated by mechanisms and circumstances such as changes in the physical habitat, hydrological regime, physico-chemical characteristics and connectivity, as well as induced effects on populations and genetic and ecosystem impacts.

Figure 1 sets out the various stages in the process leading to a biological invasion and the potential management options. The different research approaches and actions are also outlined.

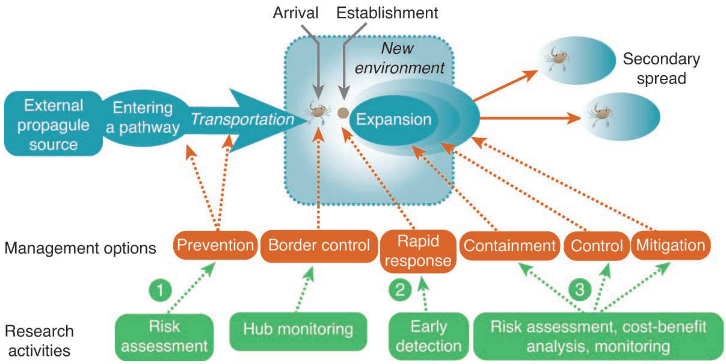

Figure 1. Typical diagram of a biological invasion process (in blue) and the different ways in which it can be managed (in orange), as well as research activities in response (in green).

Source: based on Olenin *et al.*, 2011 blue crab illustration: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library) (https://creativecommons.org/licenses/by-sa/4.0/), with permission from Elsevier.

A theoretical but realistic example illustrates the point: a merchant ship takes on its cargo in the port of Baltimore (USA) and stabilises its buoyancy by ballasting with seawater from the port. In fact, it simultaneously takes on many species that are present locally. It then crosses the Atlantic and arrives in Le Havre, France, where it unloads its cargo and changes the water in its ballast tanks (Arrival). The species are released in the port, where only a fraction survive the new environmental conditions. However, in the absence of natural controlling factors in this new environment, like predation, parasitism or even disease, a small fraction will not only survive, but will reproduce, developing a local population (Settlement) and potentially become invasive (Propagation). Another vessel will later contribute to the dispersal of these exotic species to another destination by the same processes (Secondary dispersal), where they will weaken the ecosystem and local biodiversity as a result of their proliferation. In terms of management, ballast water treatment on board can limit the initial introduction (Prevention).

Failing that, an operational surveillance network (Monitoring) organised at the level of the port can rapidly detect new species known to be invasive and initiate an action plan (Rapid Response) as long as the IAS population remains limited in number and surface area. Beyond that, more extensive containment measures (e.g. closing locks to isolate a basin) are still possible. Failing that, the management options will be reduced and will focus solely on limiting the development of populations (reduction, annual destruction management plan). For research activities, the priorities are to understand the processes involved in controlling the vectors of introduction, for example defining protocols and standards for treating ballast water and assessing the risks in order to prioritise the species to be targeted. Operational surveillance strategies (e.g. protocols, identification, sampling effort, prioritisation of introduction sites/points, new eDNA technologies) and rapid response (treatment protocols/eradication strategies) are all scientific elements that can be made available to managers to facilitate decision-making and contribute to the development of public policies (Olenin *et al.*, 2009; 2011).

Different situations may arise, depending on the species and environment concerned. In particular, the time required for each phase can vary considerably (**Figure 2**). For example, the latency phase once the species has been introduced can be very short or last several years, or even decades. The case of the Japanese oyster drill *(Ocinebrellus inornatus*), a predator of farmed shellfish, is of interest: genetic analyses have linked the presence of this Asian species to the mass introduction of Pacific oysters in the early 1970s, although it was only identified in 1994 on Ile de Ré (Pigeot *et al.*, 2000; Martel *et al.*, 2004a). The warming of the marine environment at that time facilitated its demographic explosion, with consequent impacts on the mortality of oysters in oyster beds. The expansion phase along the Atlantic coast was facilitated by oyster farming transfers between production basins (Martel *et al.*, 2004b). In addition, some species such as the common slipper limpet (*Crepidula fornicata*) are still invasive a century after their introduction, although some geographically localised populations have declined. Conversely, other species have become 'integrated' into the natural biodiversity or are declining/disappearing after a phase of massive proliferation. This is the case of *Caulerpa taxifolia* in the Mediterranean Sea, a seaweed that declined sharply since its accidental introduction in 1984, followed by a spectacular invasion lasting until 2007, when an as yet unexplained sharp decline was observed. It should be noted that two other species of *Caulerpa*, *C. taxifolia* var. *distichophylla* and *C. cylindracea*, both of Australian origin and invasive in nature, have also appeared in the Mediterranean (Piazzi *et al.*, 2005; Picciotto *et al.*, 2016). Between these two extremes, intermediate scenarios may arise, making it more difficult for managers to make decisions and implement management schemes.

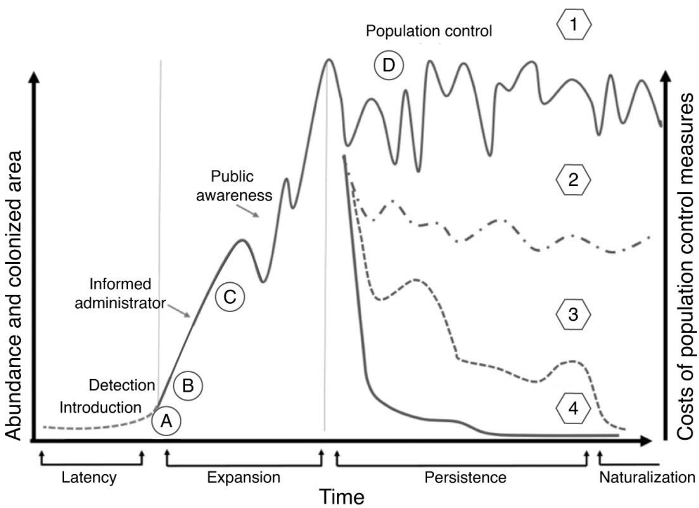

Figure 2. Temporal dynamics of a biological invasion: different types of biological invasion and potential management options. (A) Simple eradication, (B) eradication still possible, (C) eradication difficult to impossible, (D) management options only. (1 to 4) Different scenarios: from invasiveness persisting over time (1) to (4), characterised by rapid collapse followed by integration into the natural biodiversity.

Source: © 2025, Philippe Goulletquer.

WHY SHOULD WE CARE ABOUT INVASIVE ALIEN SPECIES?

The United Nations Conference on Environment and Development, better known as the Rio Summit, adopted a declaration in 1992 setting out the rights and responsibilities of countries in the field of the environment. Since then, international initiatives