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Research Article

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Abstract

An overview is presented of the Non-Indigenous Species (NIS) of algae and invertebrates recorded in the marine and brackish coastal waters of Normandy in France. Out of the 152 NIS found, 86 have been introduced through shipping (ballast waters and fouling) and 66 through aquaculture activities. A total of 95 NIS are linked to a Pacific origin and 32 come from the north-western region of the Atlantic. Among the 152 NIS identified, only nine show an invasive demography in Normandy waters. The first introductions occurred in the middle of the 19th century and became frequent by the beginning of the 20th century. However, over 50% of the NIS so far recorded were found only during the three last decades.

Key words: inventory, introduced species, invasive species, English Channel, first record

Introduction

Owing to human activities, deliberate or inadvertent introductions of species from their native ranges to new previously unoccupied areas have been on-going for thousands of years (Carlton and Geller 1993). However, these ecosystem invasions by Non-Indigenous Species (NIS) are currently considered to be one of the greatest threats to biodiversity world-wide (Vitousek et al. 1997; Mack et al. 2000). NIS represent a wide range of threats to native ecosystems; they can be responsible for the decline of native species, mainly due to competition and predation, and can cause direct economic impacts on human activities (Leppäkoski et al. 2002; Olenin et al. 2011; Katsanevakis et al. 2014; Ojaveer et al. 2014; Copp et al. 2016a, b). The assessment of species with regard to the prevention and management of the introduction and spread of invasive alien species was recently defined by the EU regulation on invasive alien species (European Commission 2014). Thus, research efforts have enabled the identification of NIS in all European sea basins in the light of continuously updated information (Leppäkoski et al. 2002; Minchin 2007; Zenetos et al. 2010, 2012, 2017; Minchin et al. 2013; Katsanevakis et al. 2013).

Unlike most chemical pollution, NIS introductions are irreversible in the marine environment and are still increasing due to the globalization and intensification of international maritime traffic and recreational boating (Katsanevakis et al. 2013, 2014; Galil et al. 2015, 2017). Nevertheless, numerous introductions have occurred without any impact on indigenous communities; these species may be harmlessly integrated into the ecosystems, and even contribute to enriching the biodiversity (Bailey et al. 2020; Goulletquer 2016).

Inventories of NIS remain an important scientific topic at the scale of the world-wide ocean, i.e. for seaweeds and macroalgae (Williams and Smith 2007; Trowbridge 2006), as well as at the scale of seas such as the Mediterranean and Baltic (Leppäkoski et al. 2002; Zenetos et al. 2010, 2012, 2017; Olenin et al. 2011; Katsanevakis et al. 2014; Copp et al. 2016a, b; Galil et al. 2015, 2017; Occhipinti-Ambrogi et al. 2011; Tsiamis et al. 2019). Such studies are also necessary at a country scale for national regulations and even at a smaller scale such as for example French regional Watershed Agencies (Goulletquer et al. 2002; Dewarumez et al. 2011; Goulletquer 2016).

Since 2010, inventories of NIS species have been published in scientific journals for many marine areas, e.g. for European waters (Katsanevakis et al. 2015), the Mediterranean Sea (Zenetos et al. 2010, 2012, 2017; Galil et al. 2015, 2017), Tunisian coastal areas (Ounifi-Ben Amor et al. 2016), British waters (Minchin et al. 2013), the Channel Islands (States of Jersey 2017), the Belgian coastline (Lescrauwaet et al. 2015), and French coastal areas (Goulletquer 2016). At the French scale, regional inventories including Brittany (Blanchard et al. 2010), the Opal Coast (Dewarumez et al. 2011) and waters around Le Havre harbour in Normandy, (Breton 2014) have been done.

The objective of this study is to provide the first inventory of marine and estuarine NIS recorded along the Normandy coastline in France. The date of the first observation in Normandy is given, as well as available information about the vectors of introduction. The list is reviewed in comparison with results from neighbouring coastal areas along the English Channel (including southern England, Brittany and the Opal coast) to identify potential new colonizers for the Normandy waters.

Materials and methods

Main characteristics of the Normandy coast

The English Channel, known as “La Manche” in French, is an important stretch of water shared between the United Kingdom to the north and France to the south. It extends for about 750 km along its principal WSW–ENE axis covering an overall surface area of ~ 77,000 km^2. Located between

48°30′N and 51°10′N, this is a temperate sea and a biogeographical transition zone between the Lusitanian and Boreal regions. This stretch of water can be divided into two distinct areas based on geographical, oceanographic and human factors, corresponding to the Western Basin and the Eastern Basin of the English Channel (Dauvin 2019). The Western Basin is influenced by Atlantic waters and the presence of a summer thermocline off the coast of Plymouth, while the Seine River mainly affects the characteristics of the Eastern Basin of the English Channel. The seawater temperature ranges between 5 °C and 20 °C in the Eastern Basin, and between 7 °C and 16 °C in the Western Basin. Salinity is higher in the Western Basin of the English Channel and in the central part of the Eastern Basin of the English Channel (> 35) than along the coastline regions.

The Normandy coastline extends over 650 km from the Normano-Breton Gulf in the West to the Bay of Seine and the coastline of the Seine Maritime Department in the East (Figure 1A). Moreover, Normandy is a transport hub for many North-European countries; both the harbours of Le Havre and Rouen have an international importance while those of Cherbourg, Caen and Dieppe have a national importance (Dauvin 2019). These same maritime transport centres also represent the main sources of NIS in Normandy coastal waters (Breton 2014; Guyonnet 2015; Berno et al. 2018). In addition, aquaculture (mussels, manila clam and Japanese oyster production) are also well developed in Normandy, especially along the coastline of the Manche Department (Dauvin 2019).

NIS inventory methods

The current inventory of NIS in Normandy coastal waters is based on three approaches.

1) The compilation of historical information from scientific journals, bulletins and the proceedings of academic societies. Historical records were analysed at national and regional levels, providing a major source of extremely rich but little known data which are sometimes not readily accessible (Table 1). The Caen University Library (Sciences and Humanities) gathered together the majority of the archives relating to Normandy, in addition to the proceedings of various academic societies, some of which are still active. A total of 1,354 sources were used to check and list the occurrences of newly introduced species in the waters around Normandy, France and Europe (Table 1). Bulletins formerly published in French by learned societies include valuable records mainly of sporadic observations ranging from species inventory at a given site to the detailed description of a newly observed species; some specimens were kept in an aquarium to study their complete life cycles.

Unfortunately, following the Second World War, there were no surviving zoological and floral collections for Normandy that could be used to check the authenticity of NIS occurrence before 1940.

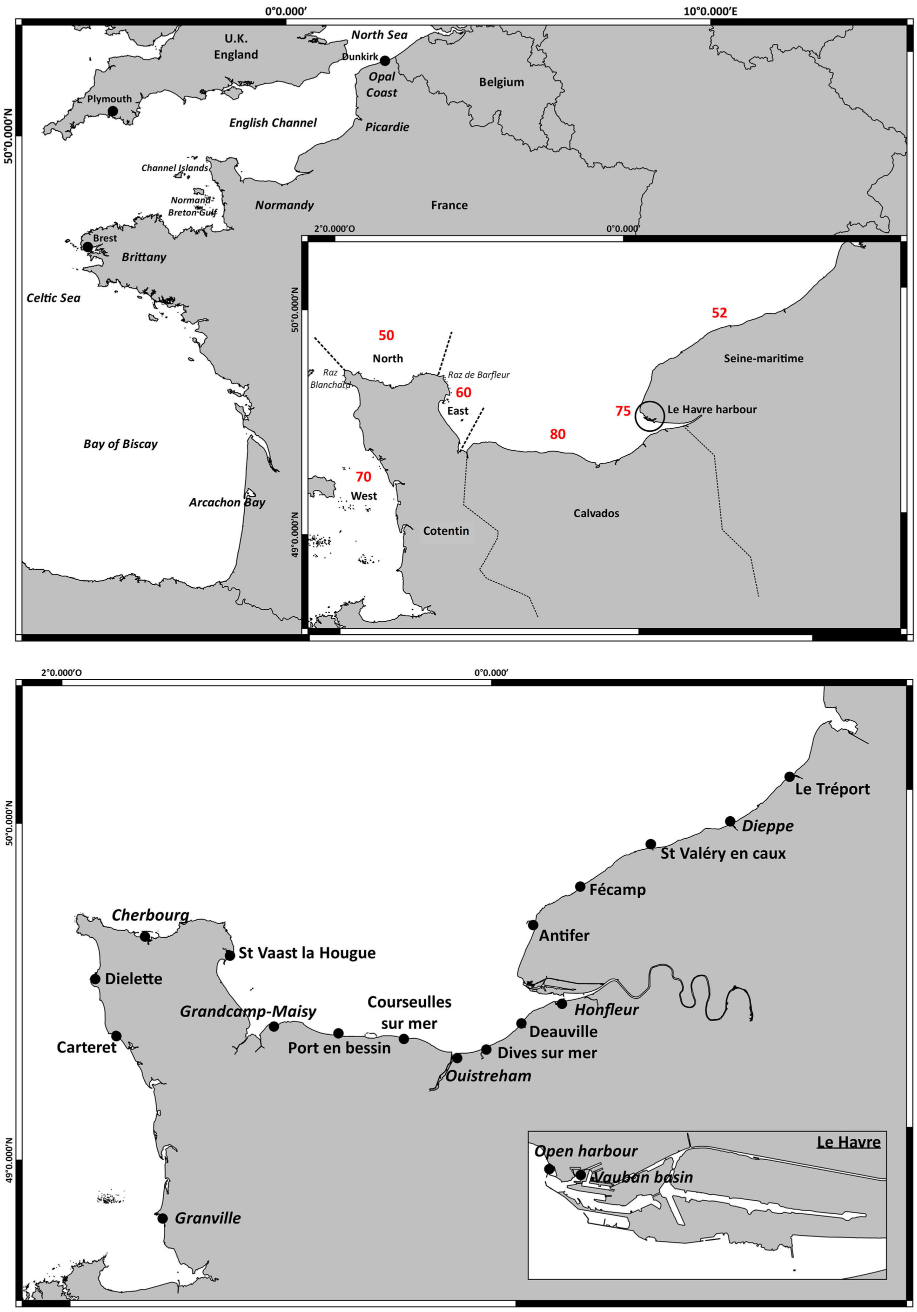

Figure 1. A, Map showing the boundaries (dashed black lines) of the study area along the French coast of the English Channel with the six sectors of the Normandy coastline (the number of NIS given in red). B, Map showing the 19 marina surveys during the EMBIMANOR project.

2) The compilation of more recent publications in international journals (consultation of databases such as web of science on 30 June 2018). Searches were made for different key-words in the indexed journals (Normandy; English Channel; Non Indigenous Species; Non-Native Species; invasive species; new record; non-autochthonous species; invader; new arrival, etc.). For the non-indexed journals, different meetings with researchers were organized to share knowledge about the literature indicating the presence of introduced species on the Normandy coast. However, it is noteworthy that these studies were not primarily aimed at detecting the arrival of NIS.

Table 1. List of journals, bulletins, and publications of academic societies consulted as sources of historical information. P, period of publication. Ny, number of year of publication and Nv, volume number.

Title	P	Ny	Nv
Mémoires de la Société Linnéenne du Calvados	1824–1825	1	2
Mémoires de la Société Linnéenne de Normandie	1826–1924	98	18
Bulletin de la Société Linnéenne de Normandie	1856–2017	160	121
Revue des Sociétés Savantes de Haute-Normandie	1956–1976	20	20
Bulletin mensuel de la Société Linnéenne de la Seine Maritime	1920–1939	19	19
Bulletin de la Société Géologique de Normandie	1873–1923	50	50
Bulletin de la Société Géologique de Normandie et des amis du Museum du Havre	1924–1972	48	48
Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre	1973–2002	29	29
Bulletin de la Société géologique de Normandie et des amis du Muséum du Havre	2004–2017	12	98
Bulletin de la Société Zoologique de France	1876–2004	128	129
Bulletin de la Société des Sciences Naturelles de l'Ouest de la France	1891–2017	125	114
Bulletin du Laboratoire maritime du Muséum d'histoire naturelle à Saint-Servan	1928–1935	7	14
Bulletin du Laboratoire maritime de Dinard	1936–1972	36	52
Mémoires de la Société nationale des sciences naturelles de Cherbourg	1852–1877	25	20
Mémoires de la Société nationale des sciences naturelles et mathématiques de Cherbourg	1879–2009	130	46
Feuille des jeunes naturalistes	1870–1914	44	528
Annales de l'Institut Océanographique	1909–2002	93	74
Bulletin de la Société des Amis des Sciences Naturelles et du Muséum de Rouen	1865–2012	147	99
Bulletin Sciences et Géologie Normandes	2009–2017	9	8

The present inventory of existing NIS in Normandy waters (Supplementary material Appendix 1) not only takes into account data concerning the Normandy coast, but also data for neighbouring areas in the English Channel. Moreover, regional-scale studies for Brittany (Blanchard et al. 2010), the Channel Islands (States of Jersey 2017) and the Opal coast (Dewarumez et al. 2011; Brylinski et al. 2012, 2016; Antajan et al. 2014; Spilmont et al. 2016) supplement the available information on NIS in Normandy and the EC.

3) The third approach consists of new sampling along the Normandy coast carried out under both the REGENI (REalisation d'un Guide sur les Espèces Non Indigènes) project and the ENBIMANOR (ENrichissement de la BIodiversité MArine en NORmandie) project. The main goal of these two projects was to compile an inventory of NIS along the Normandy coast and, more precisely, in certain particular environments (marinas).

As part of the REGENI project, seasonal surveys were organized at low tide in diverse intertidal habitats to detect the presence of new NIS in Normandy during 2016–2017 (Figure 2A, B). Furthermore, under the part of the ENBIMANOR project, field surveys were carried out to record NIS in Normandy coastal marinas (Figure 1B). One of the main goals of this project was to produce an inventory of all NIS present on the hard substrata of floating pontoons at eight marinas (Figures 1B, 2B) along the Normandy coast running from Granville in the west to Dieppe in the east. At the eight sites (Figure 2B), samples were collected by scraping the fouling community established on the hard substratum of floating pontoons, using a quadrat of 0.25 m × 0.25 m or 0.42 × 0.15 m depending on the pontoon structure (submerged pontoon surface area). Five replicates were collected from each site, each replicate corresponding to a sampling

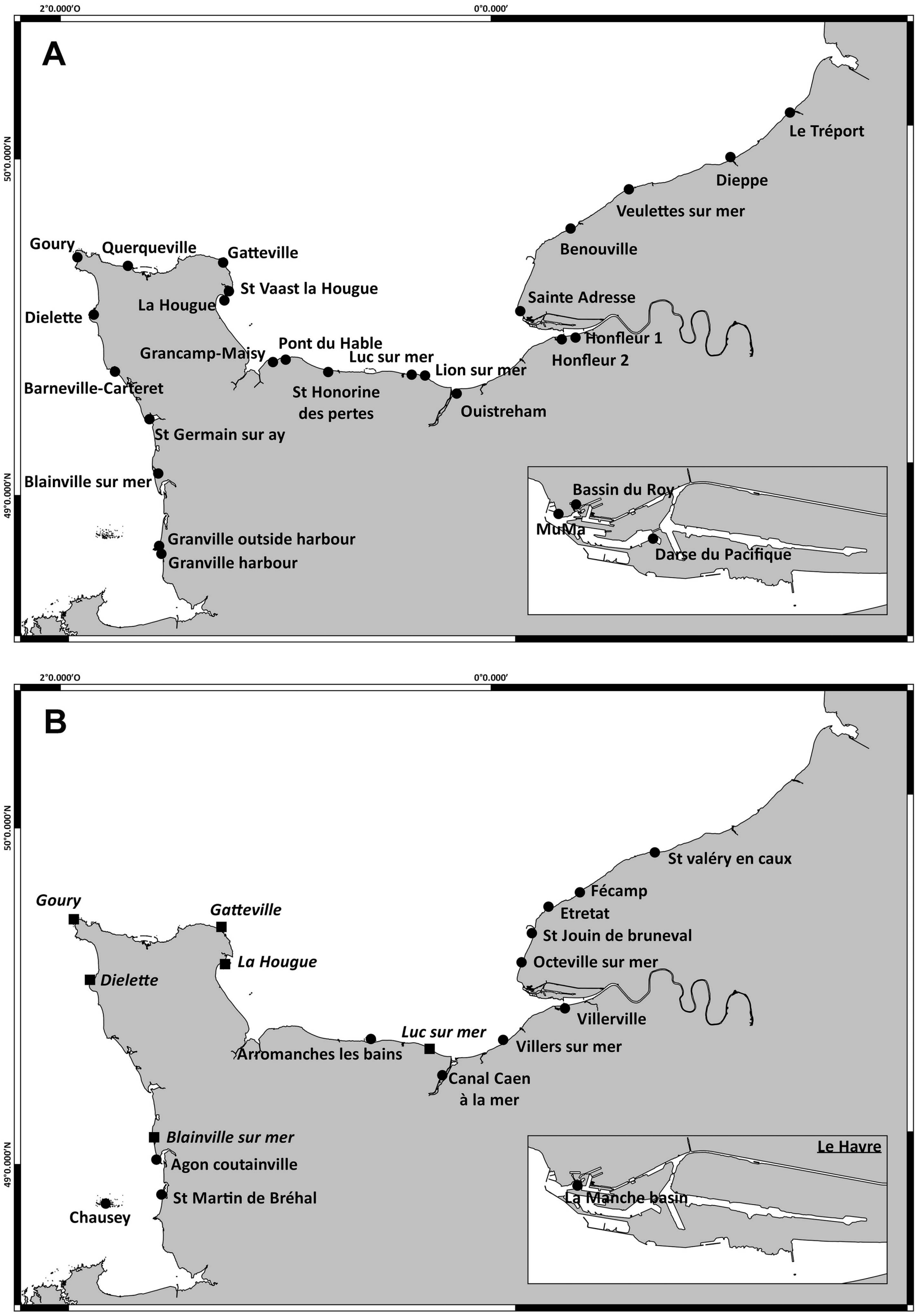

Figure 2. A, Map showing the 27 intertidal sites sampled for crab and gastropods during the ENBIMANOR project, and B, Map showing the other intertidal sites sampled to detect new NIS (the sites of *Sargassum muticum* are in italics).

surface of 0.0625 m². Approximately one hour was spent sampling different and distinct pontoon sections. Removed material was collected using a vertical plankton Work Package (WP) 2 net (200 µm) to avoid any loss of marine organisms. At Le Havre harbour, vagile fauna traps were used for shrimps, isopods and amphipods and the mobile fauna were collected by scraping the fouling community on the floating pontoons.

Finally, in April 2019, studies were carried out on the macrofauna associated with the introduced species *Sargassum muticum* (Yendo) Fensholt, 1955 (Figure 2B). The aim was to test if this seaweed known as a

Table 2. General characteristics of the six main sectors along the Normandy coast.

Sector	Coast type	Number of marinas	Number of fishing harbours	Salinity range	Temperature range	Oyster/mussel cultivation
Western coast of Cotentin	Alternation of rocky and sandy shores	3	5	34.5–35.2	8–20	yes
North Cotentin	Rocky shores	1	1	34.8–35.3	7–18	no
Eastern coast of Cotentin	Rocky shores in the north sandy in the south	2	3	34.5–35.0	6–20	yes
Calvados coast	Mainly rocky shores	8	7	34.0–34;5	6–20	yes
Basins of le Havre	Mouth of the Seine estuary	2	1	30–34	5–21	no
Seine-Maritime coast	High cliffs	5	5	31–34.3	5–20	no

refuge for motile fauna acts as an appropriate habitat for other Non-Indigenous Species in areas with dense populations of *S. muticum* around the Cotentin Peninsula. The sampling consisted of using a suprabenthic sledge with a single 0.18 m^2 box (0.6 × 0.3 m) to filter the water at approximately 0.10–0.40 m above the sea bottom in rock pools at low tide in dense *S. muticum* populations. The box was equipped with a WP2 zooplankton net (500 µm mesh size), the sledge was operated using three transects of 5 m each corresponding to a distinct sampling surface of 3 m^2 and a total surface of 9 m^2 per site.

The specimens collected in the marina fouling and *S. muticum* populations were preserved in 10% formaldehyde solution and taken to the laboratory for identification. The organisms were then sorted, identified and counted using a dissecting microscope and finally stored in alcohol.

This inventory corresponds to the NIS observed in Normandy up until 31 October 2019. As suggested by Minchin et al. (2013), we have assigned a level of certainty for the NIS recorded in Normandy following four classes: 1 – Direct Evidence, 2 – Very Likely, 3 – Possible, 4 – Unknown. The introduction pathways are stated from available information given for British waters (Minchin et al. 2013), the Brittany (Blanchard et al. 2010), the Channel Islands (States of Jersey 2017), the Opal coastline (Dewarumez et al. 2011), and the entire French Metropolitan coast (Goulletquer 2016). For the Normandy, we have taken into account the paper of Breton (2014) dedicated to Le Havre harbour which is a location of numerous first introduction of NIS in Normandy, English Channel and sometimes in European waters.

Statistical analyses

For the NIS inventory in Normandy, we analysed all the NIS species present in six geographical sectors. These six sectors correspond to areas that can be distinguished according to geography, oceanography and human activities (Figure 1A; Table 2).

Data were transformed in terms of presence-absence to analyse the spatial distribution of species in these six areas by group-average sorting classification, using a hierarchical clustering procedure (CLUSTER mode) and ordination of samples by non-metric multidimensional scaling (nMDS) based on the Sørensen similarity measure. A One-way ANOSIM (ANalysis Of SIMilarities) permutation test was used to assess if the differences between assemblages are statistically significant. The CLUSTER, nMDS and ANOSIM analyses were carried out using the PRIMER v6 software package (Clarke and Gorley 2006).

Results

NIS assessment in REGENI and ENBIMANOR projects

Several new NIS were identified including the prawns *Penaeus japonicus* Spence Bate, 1888 and *Penaeus semisulcatus* (De Haan, 1844 in De Haan, 1833–1850), both of which were recorded in the Le Havre harbour in 2016 (Pezy et al. 2017a). In 2016, the tropical crab *Guinearma alberti* (Rathbun, 1921) was found in coastal waters off the eastern part of Calvados (Pezy et al. 2017b). The bivalve *Rangia cuneata* (G.B. Sowerby I, 1832) was collected in the canal from Caen to the sea in 2017, while the mysid *Neomysis americana* (S.I. Smith, 1873) was reported in the Seine estuary in 2017 (Massé et al. 2018; Pezy et al. 2019c), and the gastropod *Stramonita haemastoma* (Linnaeus, 1767) was found along the western coast of the Cotentin peninsular in 2018 (Pezy et al. 2019a). New information is made available here on the distribution in Normandy waters of the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Pezy et al. 2015) and the blue American crab *Callinectes sapidus* Rathbun, 1896 (Pezy et al. 2019b).

In addition, sampling from the hard substrata of floating pontoons in eight marinas and also in the *Sargassum muticum* meadow has led to the recording of four new NIS for the first time in Normandy: two amphipods and two isopods. Males of the Pacific Ocean amphipod *Aoroides longimerus* Ren & Zheng, 1996 were collected at four sites on the Normandy coast (Granville, Cherbourg, Saint-Vaast-la-Hougue and Le Havre) while a second amphipod species *A. semicurvatus* Ariyama, 2004 was observed only at two sites (Granville and Saint-Vaast-la Hougue) (Dauvin et al. 2020).

About 300 specimens of the Asiatic isopod *Paranthura japonica* Richardson, 1909 were found for the first time in 2019 in Le Havre harbour (295 specimens) and Cherbourg harbour (four specimens) (Pezy et al. 2020). This species, native to the Sea of Japan, may have been introduced to the English Channel through the accumulated fouling of the hulls of ships used primarily for recreational activities.

Finally, a total of 189 specimens of the North-West Pacific Ocean isopod *Ianiropsis serricaudis* Gurjanova, 1936 were found for the first time in 2019 in Le Havre harbour (Raoux et al. 2020).

Status of NIS in Normandy

A total of 152 NIS from 17 phyla have been listed for Normandy (Appendix 1); 37 of these species are arthropods (mainly barnacles, amphipods

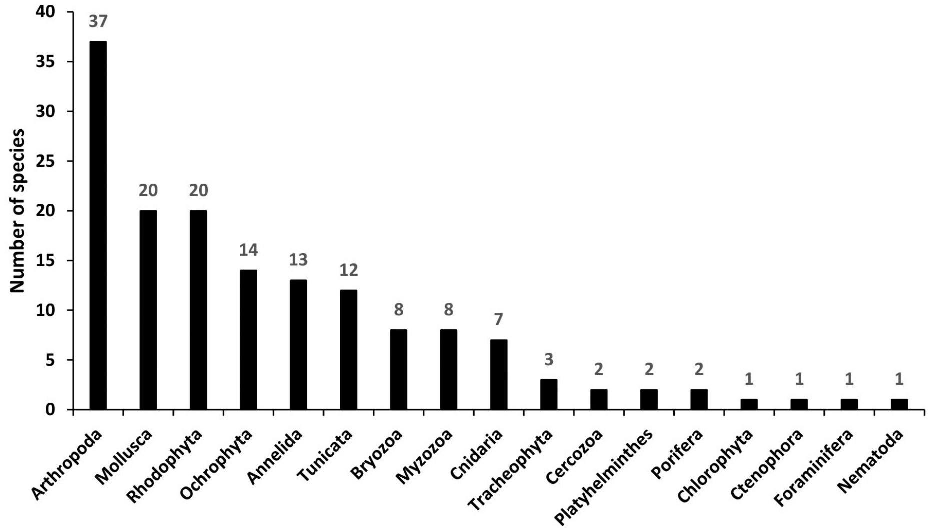

Figure 3. Taxonomic breakdown of Non-Indigeneous Species found in brackish and marine environments along the coast of Normandy, France.

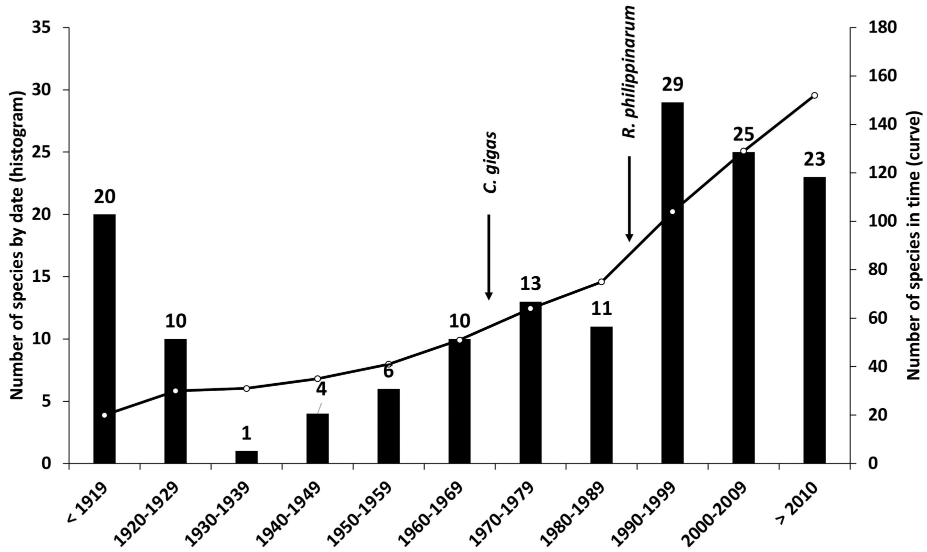

Figure 4. Non-Indigenous species introduced into Normandy waters, listed as follows: before 1919 and then introduced over 10-year intervals running from 1920 to the present day (histogram) and evolution of number of Non-Indigenous species before 1919 up to the present day (curve).

and decapods), 20 are molluscs and 20 rhodophytes (Figure 3). Three other phyla account for at least 10 species each: ochrophyta (14), annelida (13) and tunicates (12); all the other groups are represented by fewer than eight species (Figure 3), with 2/3 of the species being animals and 46 species primary producers (mainly composed of phytoplankton, macroalgae and macrophytes).

The first record of NIS in Normandy waters dates back to 1851 (Appendix 1); only 20 species were subsequently recorded up to 1919 (Figure 4). The numbers of new records remained relatively low for the period 1920 to 1989, and then became very high during the three last decades since 1990, with 77 records representing over half of all NIS known in the area (Figure 4).

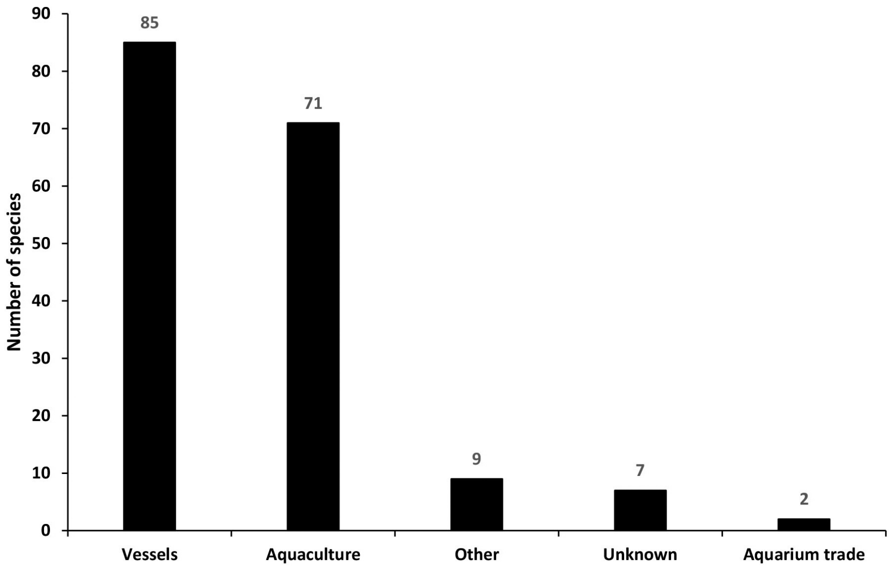

Figure 5. Pathways involved in the introduction of Non-Indigenous Species in Normandy. Other: other pathways of introduction.

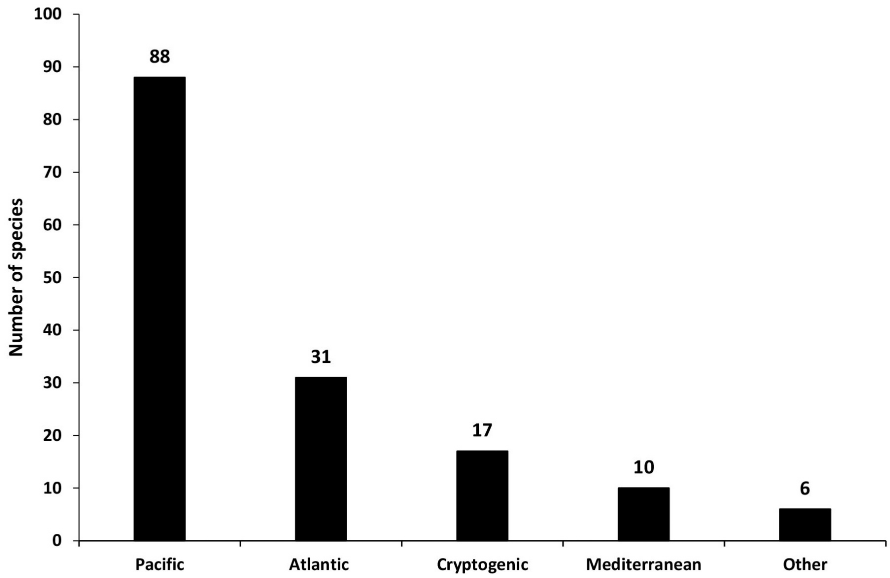

Figure 6. Geographical origins of the recorded Non-Indigenous Species in the Normandy marine environment.

Maritime traffic and aquaculture represent the two main pathways involved in the introduction of NIS in Normandy coastal waters (Figure 5); these pathways are assumed to be similar to those proposed in neighbouring regions: Brittany (Blanchard et al. 2010), Channel Islands (States of Jersey 2017), Opal coast (Dewarumez et al. 2011) and the UK coast (Minchin et al. 2013). Most of the species have a Pacific origin (88 species), followed by 31 Atlantic species and 17 cryptic species, while less than 11 NIS recorded in Normandy have a Mediterranean origin (Figure 6).

Distribution of NIS in marine and coastal waters of Normandy

The number of NIS varies along the Normandy coast from a total of 50 species in the North Cotentin to a maximum of 80 along the Calvados coast

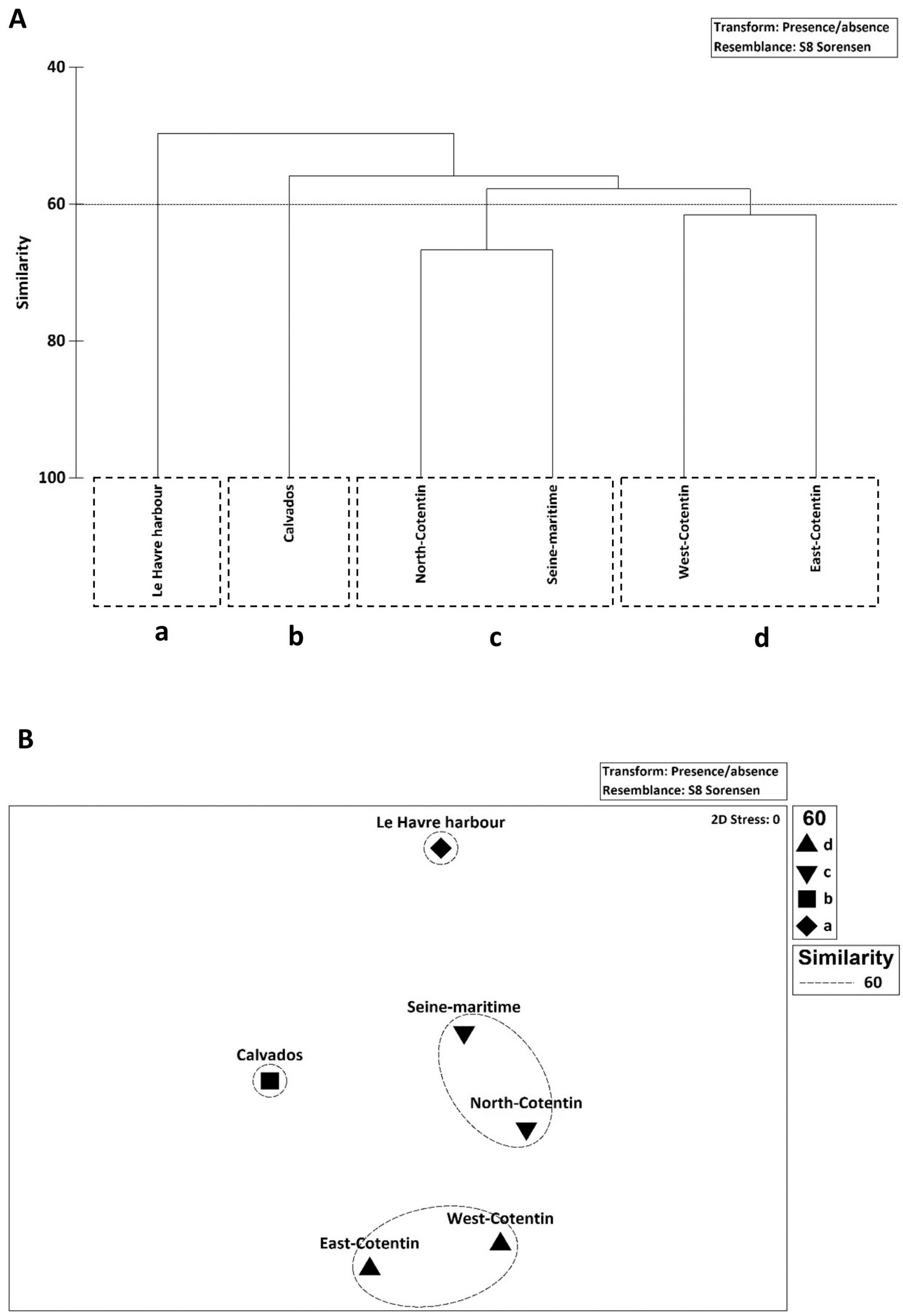

Figure 7. A, cluster dendrogram and B, nMDS ordination plot, using group averages as clustering mode, showing the Sørensen similarity coefficient (60%) on number of species over six sectors of the Normandy coastline.

(Figure 1A). The number of species along the Seine-Maritime coast is similar to that recorded in the North Cotentin with 52 species, while the numbers along the eastern coast of Cotentin and in Le Havre harbour are 60 and 75, respectively. The geographical distributions of the 152 NIS recorded from the Normandy coast (Appendix 1) in the six areas distinguished here were examined using the Sørensen coefficient and with CLUSTER and nMDS analysis (Figure 7). The six areas can be clustered into four main groups on a level of 60% similarity (ANOSIM test, $R = 0.92$; $p = 0.022$). Le Havre Harbour and Calvados form two groups, while the other

Table 3. Number of Non-Indigeneous Species found in each of the four groups of the CLUSTER analysis, with indication of the main pathways of their introduction to Normandy.

Pathways	Le Havre harbour	Calvados	North Cotentin/Seine maritime	West Cotentin/East Cotentin
Aquaculture	28	32	35	51
Vessels	50	47	41	45
Aquarium trade		2		
Other	8	3	2	5
Unknown	2	2	1	1

groups include West and East Cotentin in one case and North Cotentin and Seine-Maritime in the other.

Results show that a maximum of NIS (counted in these four groups) are found in the West and East Cotentin, followed by the Calvados, then the Le Havre harbour and finally the North Cotentin and Seine Maritime (Table 3). The main pathway is identified as "Aquaculture" for West and East Cotentin, while "Maritime traffic" dominates in the three other groups, mainly in Le Havre Harbour where it represents nearly 60% of the introduction of NIS.

Discussion

New arrivals

The English Channel is among the most impacted ecosystems in the world (Halpern et al. 2008), being subject to a high and growing number of anthropogenic disturbances, mainly in relation to the Seine estuary and the presence of two large harbours, Le Havre and Rouen, which have intense maritime traffic. The English Channel is also affected by spoil deposition linked to regular dredging of the navigation channel (Pezy et al. 2018) as well as aggregate extraction. In addition, there are many fisheries and recreational boating activities and a real practice of recreational shellfishing (mainly mussels and cockles) on the Normandy coast (Baffreau et al. 2017). Finally, the English Channel is a NIS hot spot (Baffreau et al. 2018).

This study, based on the work of Baffreau et al. (2018), is the first complete inventory of NIS in Normandy. Most of the NIS identified here are invertebrates including sessile and mobile species. The arthropoda are dominant among the NIS, with three main zoological taxa including sessile fauna such as barnacles and mobile fauna such as amphipods and decapods. Among these 152 NIS, only nine species are currently invasive in Normandy (Baffreau et al. 2018): *Bonamia ostreae* Pichot, Comps, Tigé, Grizel & Rabouin, 1980, *Crassostrea gigas* (Thunberg, 1793), *Crepidula fornicata* (Linnaeus, 1758), *Ficopomatus enigmaticus* (Fauvel, 1923), *Hemigrapsus sanguineus* (De Haan, 1835), *Mnemiopsis leidyi* A. Agassiz, 1865, *Ruditapes philippinarum* (Adams & Reeve 1850), *Sargassum muticum* (Yendo) Fensholt, 1955 and *Styela clava* Herdman, 1881) (for more details, see Baffreau et al. 2018).

Most of these invertebrate species have a bentho-pelagic development with sometimes a long larval planktonic phase which ensures their survival in ballast waters and their dispersal due to strong tidal currents such as in the English Channel. But some species i.e. amphipods and isopods have direct development and represent about 10% of the NIS (13 species); for these species, hull fouling is probably the major vector of introduction.

Long-term changes

The first record of an NIS in Normandy waters dates back to the middle of the 19th century in 1851. In the 70 years from 1950 to 1919, only 20 species were recorded, mainly in the brackish waters of the canal from Caen to the sea (Figure 4). The numbers of new records remained relatively low during the 70 years from 1920 to 1989, and then increased dramatically over the three last decades (1990–2019), with 77 records representing over half of all NIS known in Normandy (Figure 4). This result could be explained by the increase in maritime traffic and/or the deliberate introduction into France of the Japanese oyster *C. gigas* and clam *R. philippinarum*, which have been responsible for the introduction of numerous NIS (Stiger-Pouvreau and Thouzeau 2015). However, this apparent surge in numbers may be due to (1) the increase of scientific interest for NIS at the worldwide ocean scale since the turn of the 21st century under the OSPAR convention and the European MSFD in the shallow waters of the north-eastern Atlantic, and (2) the increase of sampling and taxonomic research efforts on hard bottoms, covering many of the NIS found mainly in Le Havre harbour basin (Breton 2005, 2014).

Moreover, our study revises the dates of first introduction in Normandy, and more widely, for all of France and sometimes for Europe as well. The barnacle *Amphibalanus amphitrite* (Darwin, 1854) was reported for the first time in Europe and more precisely in Spain in 1934 by Bishop (1950), but its first observation dates back to 1886 in Normandy in the canal from Caen to the sea. The mussel *Mytilopsis leucophaeata* (Conrad, 1831) was mentioned in 1913 in the Caen Canal, but was in fact first observed several years earlier in 1898 also in Normandy. However, a recent study reveals that this species was first recorded in the United Kingdom before 1866, based on specimens in old collections (Oliver 2015). The hydrozoa *Cordylophora caspia* (Pallas, 1771) was reported for the first time in 1901 at the Loire estuary. However, it was for the first time observed in 1886 at Ouistreham in Normandy. The Rhodophyta *Bonnemaisonia hamifera* Hariot, 1891 was reported for the first time in Europe in England (Isle of Wight) in 1893, but its first observation dates back to 1876 in Normandy in Chausey archipelago. So, two records revised the introduction date in France (*Mytilopsis leucophaeta* and *Cordylophora caspia*) and two in Europe (*Amphibalanus amphitrite* and *Bonnemaisonia hamifera*).

Regional peculiarities of NIS introductions in Normandy

Comparing our inventory (152 NIS) with others, we find that around 90 NIS have been recorded in marine and brackish UK waters (Minchin et al.

2013), 95 in Brittany waters (Blanchard et al. 2010), 62 species along the Opal coast (Dewarumez et al. 2011), and 73 in Belgian marine waters (Lescrauwaet et al. 2015). The sea off Normandy appears to be heavily colonized by NIS in regard to the North-Eastern Atlantic region. However, the methods differ from one area to another; our efforts to search for species has increased the number of NIS records in Normandy, whereas other studies were based solely on the literature. Moreover, the size of the studied areas could have an effect on the records. While the Opal and Belgian coastlines are shorter compared with Normandy, the lengths of the UK and Brittany coastlines are of the same order of magnitude as in Normandy and the numbers of NIS are 33% less than those recorded in Normandy.

As observed for other European countries (Minchin et al. 2013), the main pathways involved in the introduction of NIS in Normandy coastal waters are maritime traffic and aquaculture (Figure 5; Appendix 1). For Normandy, Le Havre is the main site of NIS introduction (Breton 2014; Pezy et al. 2017a). Numerous NIS have a Pacific or Indo-Pacific origin (56%) (Dauvin et al. 2019). Fewer originate from the Atlantic, and these mostly from the north-western Atlantic (Figure 6; Appendix 1). Only few species come from the Mediterranean Sea.

As reported by Breton (2014), the basins of Le Havre harbour act as a pioneer site for the settlement of many NIS at the scale of Normandy (Figure 1). The exploration of Le Havre harbour by scuba diving from 1978 to 2012 has allowed the recording of 364 animal species, of which 36 are NIS. Similarly, Verlaque and Breton (2019) have examined the marine macroflora of the Le Havre and Antifer harbours by citizen scientists since the late 1970s. A total of 97 and 62 macroalgae were identified, respectively in Le Havre and Antifer, including 14 NIS. These authors (2019) point out that, as opposed to animal species, no new NIS of primary producers have been detected for the NE Atlantic since the late 1970s. For 2019, our inventory reports 75 NIS (fauna and flora) for the Le Havre harbour, including phytoplankton and new records obtained during our recent sampling (Appendix 1).

However, the number of NIS along the Calvados coast (80) is higher than for Le Havre (75), for three reasons: 1) the size of Le Havre harbour at Le Havre is smaller than the studied area of the Calvados coast, 2) the spread of NIS firstly recorded in the Harbour basins, carried by currents towards the Calvados coast, and 3) some NIS are introduced via oyster culture along the Calvados coast, while no aquaculture is developed in the area of Le Havre Harbour.

Concerning aquaculture, the oyster *C. gigas* was voluntarily introduced in the Atlantic coast of France in the 1970s to replace the Portuguese oyster *Crassotrea angulata* (Lamark, 1819), which had completely disappeared by the end of the 1960s due to a disease (Stiger-Pouvreau and Thouzeau 2015;

Goulletquer 2016). The risks arising from the reproduction and dispersal of *C. gigas* through French and European waters were not evaluated at the time of its introduction, nor the risks of accidental colonization of numerous NIS along with oyster cultivation. It appears that the West and East Cotentin coasts, two areas of oyster cultivation, show closely similar patterns of colonization by NIS (Figure 7); aquaculture is considered as the main pathway of introduction in these areas.

The NIS *Sargassum muticum*, commonly known as Japanese wireweed, is a large brown seaweed now present on the west coast of the Cotentin peninsular and along the coastline of the Calvados department, especially in areas of shellfish farming. It is known to occur on much of the western coasts of Europe from the south of Spain to southern Norway although seemingly absent from the eastern coasts of the United Kingdom (Belsher and Pommellec 1988). Furthermore, dense populations of *S. muticum* can also act as a protection area for many vagile species, such as some fish, the shrimp *Palaemon serratus* (Pennant, 1777), amphipods, isopods and cephalopods. *Sargassum muticum* produces a favourable habitat for other NIS such as the amphipods *Aoroides longimerus* and *A. semicurvatus* found among this macroalgae at Saint-Vaast-la Hougue (East Cotentin) during sampling in spring 2019 (Dauvin et al. 2020).

Nevertheless, it is often difficult to identify the real origin and pathway of an introduced species. In some cases of possible misidentification of a species, it proves useful to re-examine the collected material. This situation applies to the amphipod *Monocorophium uenoi* (Stephensen, 1932), which was reported for the first time in Europe on the coast of the Netherlands in 2013, even though it had already been recorded as being present (at least since 2007) in the Arcachon Bay in France (Gouillieux and Massé 2019). However, new genetic approaches have emerged as a useful tool to identify the origin of introduced species in Normandy. Makino et al. (2018) show that the population of the Asian brush-clawed shore crab *Hemigrapsus takanoi* Asakura and Watanabe, 2005 found in the Bay of Seine consists of a genetic mixture of populations from Japan and the Yellow Sea off the coast of China. Molecular methods have been used used to identify the origin of *Paracaprella pusilla* in European and Mediterranean waters (Cabezas et al. 2019). Metabarcoding has also been applied to elucidate invasion processes mainly on tunicate species (e.g. Comtet et al. 2015). As highlighted by Marchini and Cardeccia (2017), NIS amphipods offer a wide spectrum for future taxonomic research on cryptogenic species, unresolved taxonomy and overlooked introductions.

Moreover, the use of recent molecular techniques now enable the identification of new species from complex or cryptogenic species (Hanson et al. 2012; Nezan et al. 2014). All these new techniques and approaches offer new possibilities to increase our knowledge of NIS not only in Normandy and in the English Channel, but more largely in the worldwide. As a result, future studies on NIS should involve collaborations between ecologists (sampling, morphological identification of species) and molecular biologists.

Conclusion

In total, 152 NIS have now been recorded in Normandy. Among these, 11 species were reported more than a century ago or are difficult to observe (microalgae and unicellular organisms) and their presence needs to be confirmed. Moreover, about 90 other species have been observed in neighbouring areas: in Brittany and the Opal Coast (north of France), as well as on the coasts of southern England, Belgium and northern Germany. Secondary spread from these populations in neighbouring areas is a potential future pathway: their presence could be confirmed in the coming years. The sea off Normandy appears to be one of the hotspots of NIS in Europe. Two principal pathways have contributed to this situation: international maritime transport (with two main ports at Le Havre and Rouen in the Seine estuary), and the development of aquaculture since the 1970s in the region, principally due to the introduction of the Pacific oyster *Crassostrea gigas* and its spread from oyster farms not only along the local French coast but extending further to the waters around the British Isles.

Future research will need to focus on two main objectives concerning NIS in Normandy: monitoring introduction hotspots (e.g.: marinas, commercial ports, fish farms and shellfish farms) and molecular approaches to ensure the correct identification of NIS and cryptogenic species, and to determine their origin. Some of these objectives are being addressed in the framework of the ENBIMANOR programme, which continues until spring 2021, mainly to monitor the species present in Normandy marinas. During this programme, a collection of NIS in Normandy was initiated. Material is being stored in alcohol awaiting the start of national and international collaboration using a barcoding approach in the future.

Finally, with the future implantation of Offshore Wind Farms along the Normandy coast (Raoux et al. 2017; Pezy et al. 2018), the monitoring of NIS remains crucial as they could act as stepping stones or corridors for invasive species (Wilhelmsson and Malm 2008; Raoux et al. 2019) and could therefore be responsible for changes in the ecosystem structure and functioning.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. NIS inventory in Normandy.

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