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An Overview of Marine Non-Indigenous Species Found in Three Contrasting Biogeographic Metropolitan French Regions: Insights on Distribution, Origins and Pathways of Introduction

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Abstract: Biological invasions are one of the main global threats to biodiversity in terrestrial, freshwater and marine ecosystems worldwide, requiring effective inventorying and monitoring programs. Here, we present an updated list of non-indigenous species in French marine and transitional waters. Focused on eukaryote pluricellular species found throughout the three metropolitan French marine regions (Western Mediterranean Sea, Bay of Biscay and the Northern Seas), a total of 342 non-indigenous, including 42 cryptogenic, species are listed as having been introduced since the 13th century. The majority of the species originated from the temperate Northern Pacific. They mainly arrived through both ballast and hull fouling and also are associated with shellfish farming activities. Most of them have been introduced since the 1970s, a time when maritime and aquaculture trade intensified. Despite important human-aided opportunities for species transfer between the three marine regions (for instance, via recreational boating or aquaculture transfers), only a third of these NIS are common to all regions, as expected due to their environmental specificities.

Keywords: species introductions; inventory; biogeographic provinces; maritime trade; aquaculture; France; baseline; MSFD

1. Introduction

Non-indigenous species (NIS) introduction rates have escalated over the last century, at a global scale, due to the ever-increasing globalisation of trade and transportation [1,2]. Only a small fraction become invasive alien species (IAS, i.e., NIS showing significant negative impacts as defined by European Union Regulation No 1143/2014), noticeably inducing a wide range of ecological and socio-economic damages, including the large-scale homogenisation of biological diversity [3] as well as impacts on human health [4] and the economy [5]. As a consequence, IAS have been identified as one of the five main direct drivers of biodiversity change by the Convention on Biological Diversity (CBD) since 2000 and, more recently, by the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES 2019) [6]. Non-indigenous species are, therefore, the subject of descriptive and applied research, as well as the target of a range of regulations and policies. In France, they are central to the objectives of a long-standing research network (Groupement de Recherche, GDR) entirely dedicated to "Biological Invasions" as well as an "Invasive Alien Species (IAS) Resource Center" (IUCN/OFB; https://especes-exotiques-envahissantes.fr/ accessed on December 2022) intended to promote exchanges between researchers, policy-makers, managers and stakeholders and to provide resources for better IAS management. Moreover, a national strategic plan published in 2017 and implemented through an action plan to prevent both the introduction and spread of invasive NIS was launched in 2022 (https://www.ecologie.gouv.fr/lancement-du-plan-daction-prevenir-lintroduction-et-propagation-des-especes-exotiques-envahissantes accessed on December 2022).

In marine and transitional environments, management and, in particular, eradication of invasive species are extremely challenging, with very few successful examples to date (see examples in [7]). Regulations have therefore prioritised efforts to prevent NIS introductions or to reduce their spread at an early stage of introduction [7], both of which require dedicated monitoring programs. As an EU Member State, France implements the Marine Strategy Framework Directive (MSFD—Directive 2008/56/EC) [8]. Under this directive, descriptor 2 (D2) is dedicated to NIS, aiming to reduce and, ideally, stop their introduction. The primary criterion for this descriptor is the number of new NIS, which must be reported by each of the European Member States. However, to control progress towards this achievement, not only is accurate monitoring required, for instance, by relying on the taxonomic expertise of the operator, but also robust and reliable baselines are needed [9] with the ultimate aim of minimising uncertainties and errors. Such a baseline was provided at the European scale in the study by Zenetos et al. [10]. As a companion paper to this study, we here provide a more detailed baseline for the French metropolitan coastline.

To consider the singularity of the French metropolitan coastline, our inventory is based upon the division into three biogeographic provinces sensu Spalding et al. [11], i.e., the Mediterranean, the Lusitanian and the Northern European Sea provinces, hereafter referred to as the French regions of (1) the Western Mediterranean Sea, (2) the Bay of Biscay (i.e., the Atlantic Ocean) and (3) the Northern Seas (encompassing the French parts of the Celtic Sea, the English Channel and the North Sea). These biogeographic regions display strongly contrasted oceanographic features (Figure 1), for instance: (1) the Mediterranean Sea has a microtidal regime and corresponds to the warmest and most oligotrophic conditions; this ecosystem is also known for hosting the largest amount of marine NIS at the European level [10,12]; (2) the Bay of Biscay, open to the Atlantic

Ocean, presents a very strong and complex hydrodynamic regime and stratified waters; and (3) the Northern Seas are also characterised by strong tidal currents and ranges, and homogeneously mixed waters because of shallower depths [13]. As expected among distinct biogeographic provinces [11], the species assemblages among these three regions are distinctive, as exemplified by Gallon et al. (2017) [14], for the species inhabiting sublittoral soft bottom habitats. Human activities are, however, important throughout, and regular trade and exchanges occur among all three provinces. In addition to trans-oceanic primary introductions, NIS movements are thus expected across these regions due, for instance, to aquaculture practices and transfers, maritime traffic or recreational boating. Aquaculture is a putatively important pathway in Europe, particularly in France, due to important shellfish farming activities [15,16]. Similarly, regional shipping and recreational vessels, two vectors that have received little attention until recently, are now recognised as major vectors of spread [17]. More recently, marine debris has been shown to be another important vector for NIS spread [18]. All these pathways can lead to secondary introductions or further spread of NIS [19,20]. We thereby expect that, regardless of the region of first introduction, NIS may spread naturally across regions and establish if they can find favourable habitats in another close region, for instance, by stepping-stone dispersal between the Bay of Biscay and the Northern Seas. In addition, due to human activities, NIS first introduced in an unfavourable habitat may finally be transported to a more favourable one, as exemplified by cold temperate species first introduced in the Mediterranean Sea finally finding favourable living conditions and thriving in the North Seas. This example holds for the kelp *Undaria pinnatifida* (Harvey) Suringar, 1873, native to the temperate north-western Pacific, which was first introduced into the Thau Lagoon (western Mediterranean Sea) but did not spread further, whereas it rapidly escaped and established populations in the English Channel (Northern Seas) following its introduction for cultivation purposes [21,22].

Within this context, we aim to provide an updated inventory of known marine and estuarine NIS and to document their attributes (taxonomy, origins and vectors), not only at the French national level but also for each of the three French biogeographic regions (Figure 1), with the main objective of providing an updated baseline for future works. We also assess whether the current regions of species occurrence are different from the region where they were first reported and whether the Mediterranean Sea displays species that are only found in these warmer waters, and, conversely, whether the two other regions with more similar environmental conditions share NIS. A final goal of this paper is to point out the uncertainties in NIS monitoring, such as those due to (1) the identification methods used, (2) systematic/taxonomic revisions and changes and (3) biogeographic uncertainties (notably regarding NIS origins). These considerations aim to provide recommendations for future monitoring networks and programmes.

2. Methodology

Previous lists of NIS found in the French metropolitan waters, published in Goulletquer et al. [23] and Goulletquer [24], were updated based on the following sources: data from scientific NIS literature (e.g., Blanchard et al., [25] for Brittany; Dewarumez et al. [26] for the Opal coast; Pezy et al. [27] for Normandy), from annual ICES French national reports (e.g., ICES 2022) [28], from the MSFD monitoring programme (under development), and from other monitoring surveys conducted as part of ongoing research projects, such as the National Observation Service of Benthic Macrofauna (SNO BenthOBS). Data were compiled and reviewed by the members of the “French D2 Expert Working Group” who authored this article.

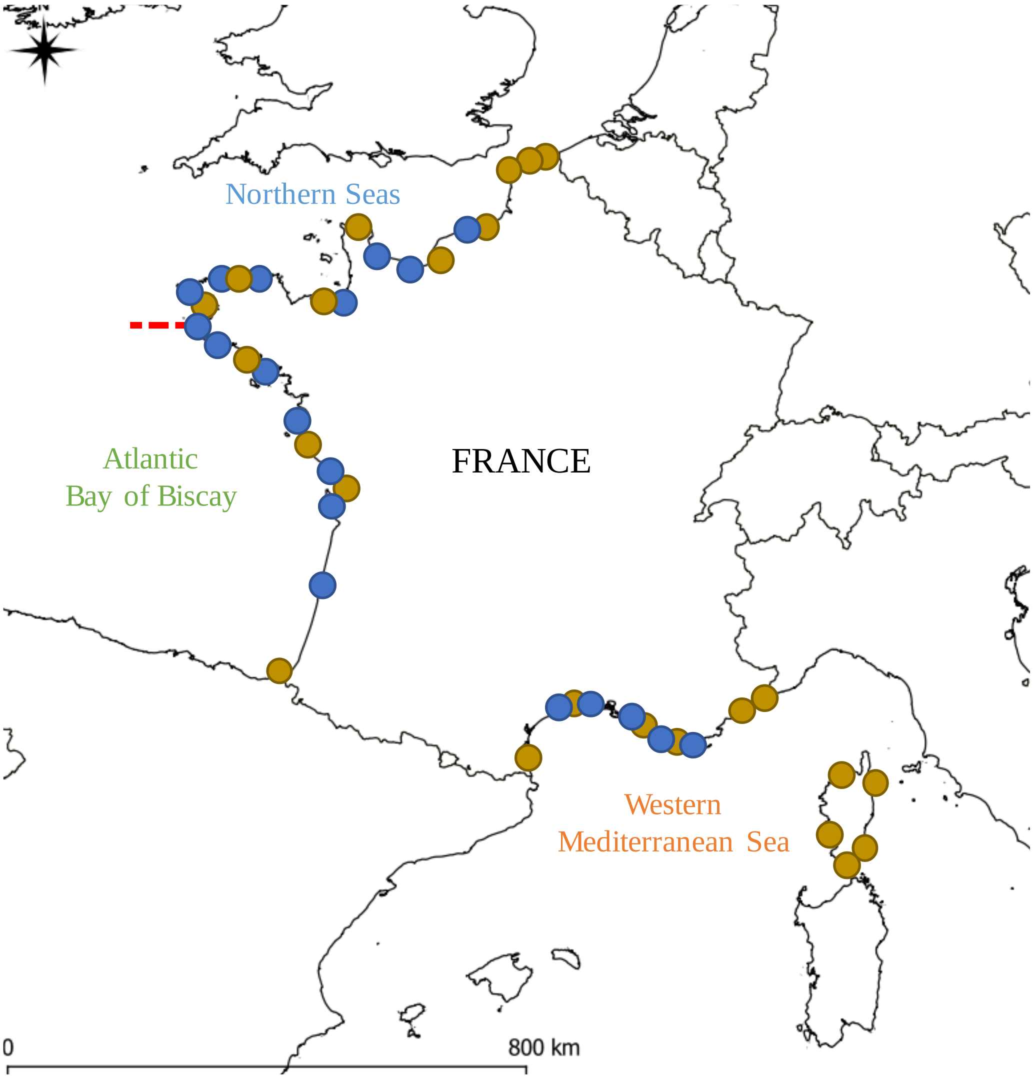


Figure 1. Delimitation of the three regions along the French coast defined for this study according to the Marine Strategy Framework Directive. Northern Seas encompass the Celtic Sea, the English Channel and the North Sea. Blue circles represent the main French sites of shellfish farming. Brown circles represent the main French ports according to the European Marine Observation and Data Network (EMODnet: https://www.emodnet-humanactivities.eu/ accessed on December 2022), based on maritime transport (goods, passengers and vessel traffic) provided by ports. Note that in 2015, 473 maritime ports with 186,000 berths were counted along the French metropolitan coastline (Department of Maritime Affairs, 2015).

2.1. Geographic Coverage

Data that were included encompass the coasts of the whole of mainland France plus the island of Corsica (i.e., metropolitan France) but exclude overseas territories. The French coastline was divided into three marine regions (Figure 1), with the border between the Bay of Biscay and Northern Seas corresponding to the administrative limit defined by the MSFD and OSPAR (Oslo-Paris regional sea convention) between the subregions of the Bay of Biscay and the Celtic Seas. Note that the term "Northern Seas" is adapted from the "Northern European Seas" of Spalding et al. [11] and corresponds to the French regions of the Celtic Sea, English Channel and North Sea.

2.2. Data Included

The dataset compiles all species observed at least once (i.e., the data includes species that are nowadays extinct), whether they were observed in an introduction hotspot (e.g., ports) or in the wild and their developmental stage (Table S1). Note that a first report does not necessarily correspond to early detection. Some, if not most species, when identified for the first time, were already widespread (e.g., the tunicate *Asterocarpa humilis* (Heller, 1878) along the Western English Channel [29]. The time period considered starts with the first known introduction in the 13th century and ends in September 2022. The number of new NIS (i.e., first reported at the French level) is reported per year, with the year of first record related to the year of first observation. In the absence of information regarding the observation date, the publication date was noted instead. In cases of temporal uncertainty (e.g., the time period is indicated as a range, for instance, "in the 1970s"), the median year is provided.

This update focuses on pluricellular species belonging to the kingdoms of Animalia, Chromista and Plantae. Information sources are provided for each species (Table S1). Cryptogenic species are included in the list, except for those species reported as currently expanding their natural range—such as those resulting from climate change. Following MSFD recommendations [9], estuarine species reported in oligohaline zones (salinity < 5) only observed in coastal waters were included. The Mediterranean Sea and the South European Atlantic Shelf regions are separated by a well-documented biogeographic barrier, the Almeria-Oran front, where phylogeographic breaks also occur [30]. Thus, for the Mediterranean Sea and Bay of Biscay regions, species native to one or the other region were included when (1) a human-assisted introduction is supported by strong evidence (e.g., the nassariid *Tritia neritea* (Linnaeus, 1758), see the Discussion section) and (2) the species was absent along the Iberian coast at the date of introduction attesting that it did not follow a natural expansion.

2.3. Species Attributes

The current status of the presence of each species in every French marine region is given, based on available data in the scientific literature, in the French National Inventory of Natural Heritage (INPN: https://inpn.mnhn.fr/accueil/index?lg=en accessed in December 2022) and on expert knowledge. According to the literature, species can be classified into seven occurrence categories: One record, i.e., observed once; Casual, i.e., very rarely observed; Established, i.e., populations are observed; Established to invasive when populations are more and more predominant in an ecosystem of the considered biogeographic region; Invasive, i.e., when a population is dominant and an impact has been documented in the literature in at least one ecosystem of the considered biogeographic region; Extinct; or Native. Note that the word "extinct" means that the species was never further reported/observed in France following its first report. There may, however, be false negative reports in case of unnoticed populations/individuals. This status also holds only for the study area, such as the three French regions here investigated, whereas the species might still be present in other European seas or elsewhere.

Regarding the NIS geographic origin, the native distribution area of the reported NIS was defined according to their biogeographic realm, as detailed in Spalding et al. [11]. For NIS originating from a European sea, the province level, sensu Spalding et al. [11], was used to get a more accurate spatial definition.

Presumed pathways of first NIS introductions in France were attributed based on the literature. The recommendations from the Convention on Biological Diversity (IUCN 2018) [31] propose six categories of pathways (Table 1): two for intentional introductions, for example, "release in nature" for NIS that were introduced to be cultivated but established beyond farms [e.g., the kelp *Undaria pinnatifida* or the oyster *Magallana gigas* (Thunberg, 1793)]; two for unintentional introductions, for example, "transport as hitchhikers", for NIS associated with intentionally introduced species (e.g., the bivalve *Anomia chinensis* Philippi, 1849 unintentionally introduced with the oyster *Magallana gigas)*; and two for introductions through corridors or secondary dispersal as exemplified by species introduced via the Suez Canal into the Mediterranean Sea.

Table 1. Pathway categories and associated vectors used in this study adapted from Harrower et al., 2018.

Type of Release	Pathway Categories	Vectors
Intentional	Release in nature	Fishery in the wild (including game fishing)
		Other intentional release
Unintentional	Escape from confinement	Aquaculture/mariculture
		Botanical garden/zoo/aquaria (excluding domestic aquaria)
		Live food and live bait
	Transport-Hitchhikers	Hitchhikers on animals (except parasites, species transported by host/vector)
		Parasites on animals (including species transported by host and vector)
	Transport-Stowaway	Angling/fishing equipment
		Hitchhikers on ship/boat (excluding ballast water and hull fouling)
		Organic packing material, in particular, wood packaging
		Ship/boat ballast water
		Ship/boat hull fouling
	Corridor	Interconnected waterways/basins/seas
	Unaided	Natural secondary dispersal across borders of invasive alien species that have been introduced

3. Results

3.1. NIS Number, Taxonomic Identity (over France and per Region) and Status

A total of 342 marine non-indigenous (n = 300) and cryptogenic (n = 42) species were introduced into French metropolitan waters (Table S1, see Data Availability Section to retrieve the list). The distribution among kingdoms is strongly unbalanced, with 70% belonging to animals, 24% to plants and 6% to chromists, and are divided into 15 phyla (Table 2). A third of them are shared across the three French regions, and 34–42% are present nowadays in at least two regions (Figure 2). The overlap is slightly higher between the Northern Seas and the Bay of Biscay (i.e., 42% of the 342 species) than between one or the other of these two regions and the Western Mediterranean Sea (i.e., 34% and 38%, respectively). Of the 342 species introduced, 14 were reported later as extinct at the French national level. For the remaining ones, their status (from extinct to invasive) is variable across regions (Table S1 and Figure 3).

Table 2. Number and proportion of NIS across phylum and biogeographic region along the French coast.

Kingdom	Phylum	Overall French Coastline	Northern Seas	Bay of Biscay	Western Mediterranean
Plantae	Rhodophyta	67 (20%)	26 (15%)	31 (17%)	59 (24.7%)
	Chlorophyta	10 (3%)	3 (2%)	2 (1%)	10 (4%)
	Tracheophyta	5 (1%)	3 (2%)	4 (2%)	2 (0.8%)
Chromista	Ochrophyta	20 (6%)	6 (4%)	6 (3%)	18 (7.5%)
Animalia	Arthropoda	69 (20%)	44 (26%)	47 (25%)	38 (16%)
	Mollusca	44 (13%)	23 (14%)	29 (16%)	25 (10%)
	Chordata	43 (13%)	18 (11%)	21 (11%)	36 (15%)
	Annelida	38 (11%)	22 (13%)	22 (12%)	18 (8%)
	Cnidaria	23 (7%)	9 (5%)	8 (4%)	17 (7%)
	Bryozoa	16 (5%)	9 (5%)	10 (5%)	11 (5%)
	Platyhelminthes	2 (0.5%)	2 (0.5%)	2 (1%)	1 (0.4%)
	Porifera	2 (0.5%)	1 (0.5%)	1 (1%)	1 (0.4%)
	Ctenophora	1 (0%)	1 (1%)	1 (1%)	1 (0.4%)
	Nematoda	1 (0%)	1 (1%)	1 (1%)	1 (0.4%)
	Echinodermata	1 (0%)	0	0	1 (0.4%)

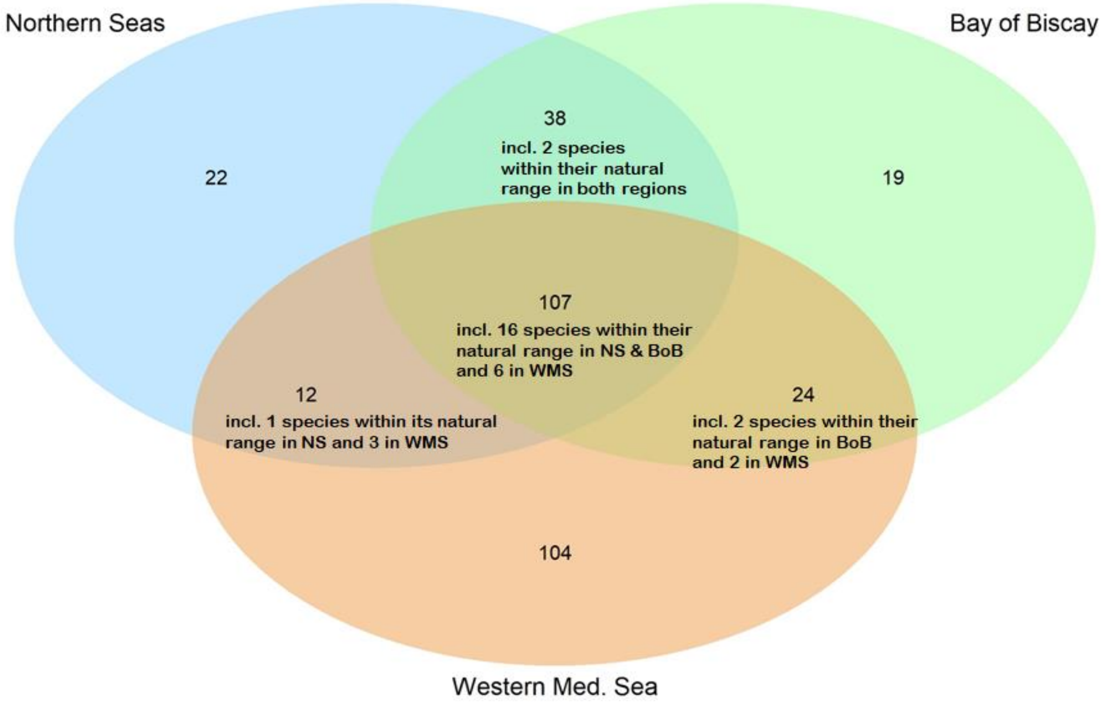


Figure 2. Venn diagram of the number of NIS exclusive to each of the three biogeographic regions and shared across regions. The numbers include species within their natural range in one region but introduced in another one, as detailed in the figure. "NS", "BoB" and "WMS" stand for Northern Seas, Bay of Biscay and Western Mediterranean Sea, respectively. Note that the status of the species considered here may be from casual to invasive (see details in Table S1).

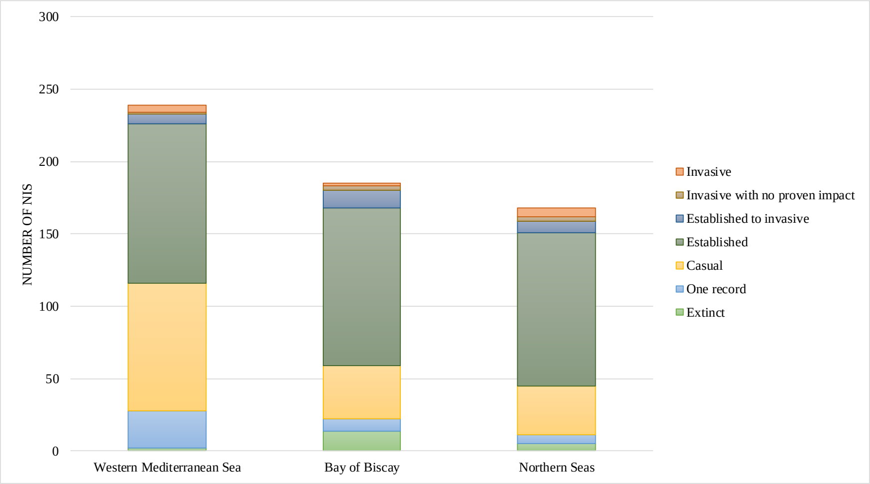


Figure 3. Number of NIS per presence status in each of the three French biogeographic regions.

Western Mediterranean Sea

Among the 342 non-indigenous and cryptogenic species, 239 (70%) were introduced along the French Mediterranean coast (204 non-indigenous and 35 cryptogenic), of which 104 are present only within this region (Figure 2). These species belong to the animal (150 species; 63%), plant (71 species; 30%) and chromist (18 species; 8%) kingdoms and are divided into 15 phyla (Table 2). The vast majority are well-established (46%) or casual (37%), with only 2% invasive in this region (Figure 3).

Bay of Biscay

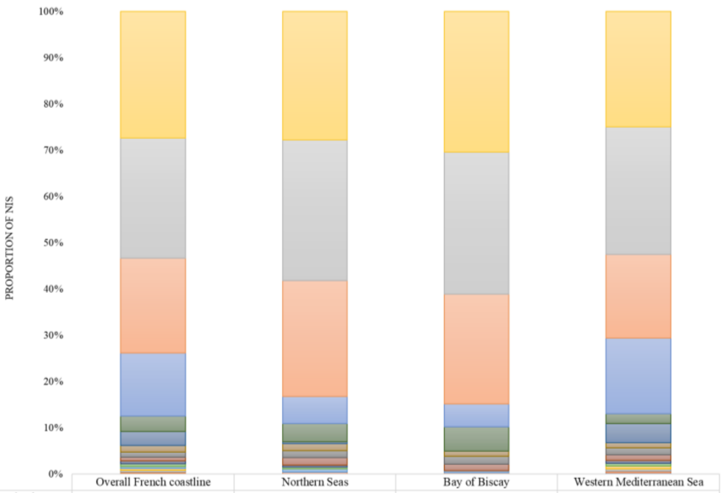
In the Bay of Biscay, 185 of the 342 (54%) species were recorded (165 non-indigenous and 20 cryptogenic species), with 19 being specific to this region (Figure 2). Non-indigenous and cryptogenic species in this region belong to the animal (142 species; 77%), plant (37 species; 20%) and chromist (6 species; 3%) kingdoms and are divided into 14 phyla (Table 2). In this region, 59% are well-established, 20% are casual and only 1% are considered really invasive (2% reported as invasive but with no proven impact) (Figure 3).

Northern Seas

In the Northern Seas, 168 of the 342 (49%) non-indigenous and cryptogenic (146 and 22 species, respectively) species were recorded, with 22 being specific to this region (Figure 2). These species belong to the animal (130 species; 77%), plant (32 species; 19%) and chromist (six species; 4%) kingdoms and are divided into 14 phyla (Table 2). In this region, 63% are established and 20% are casual, while 4% are invasive (Figure 3).

3.2. Reported Pathways and Vectors of Introduction

Of the 342 NIS recorded at the metropolitan France scale, 115 (34%) are reported as having been introduced via several pathways and vectors, with up to four pathways for the Ochrophyta *Chrysonephos lewisii* (W. R. Taylor) W. R. Taylor, 1952 (Table S1). The most represented pathway is transport stowaway (TS), with 232 species (68 %) having been probably introduced via two vectors, maritime traffic with ballast waters (29%) or hull fouling (37%) (Figure 4). However, the most represented vector is "hitchhikers on animals", with 133 species (39%) belonging to the "transport and hitchhikers" pathway (Figure 4). As expected, 14 of the 15 species (4%) introduced through a corridor were first reported in the Mediterranean Sea via the Suez Canal.



	Overall French coastline	Northern Seas	Bay of Biscay	Western Mediterranean Sea
TH - On animal	133	71	86	84
TS - Hull fouling	126	78	87	93
TS - Ballast	100	64	67	61
Unknown	66	15	14	55
R - Fishery in wild	16	10	15	7
C - waterways	15	1	0	14
U - Natural dispersal	7	4	3	4
TH - parasites	5	4	5	5
EC - Mariculture	4	4	4	4
R - Other	3	1	0	2
EC - private aquaria	3	1	0	2
TS - organic packing	2	2	1	0
TS - Hitchhikers (boat)	2	0	0	2
TS - fishing equipment	2	0	0	2
EC - live bait	1	1	1	1
EC - public aquaria	1	0	0	1

Figure 4. Proportion and number of NIS according to their pathways and vectors of introduction along the French coast. TH: transport hitchhiker; TS: transport stowaway, R: released in nature, C: corridor, U: unaided, EC: escape from confinement. The table presents the number of NIS. The total number of NIS exceeds 342 because one NIS could have been introduced through several pathways or vectors.

3.3. Biogeographic Origin of Introduced Species

Besides cryptogenic species (*n* = 42), most of the 342 species introduced along the French coasts are native to temperate areas (blue colours in Figure 5), with 65% of the 300 species having a known native range. The temperate Northern Pacific is particularly well represented (42%), followed by the temperate North Atlantic (18%). In comparison, only four species native to temperate Southern Africa, and a single species (i.e., *Ostrea chilensis* Küster, 1844, also present in New Zealand) native to temperate South America, have been recorded. Species native to temperate regions were reported in similar proportions across the three French regions (Figure S2 in Supporting Material). However, differences were reported among the three French regions for species native to the Western or Eastern Indo-Pacific regions. In fact, the 24 NIS native to those areas were all, with one exception, reported for the first time in the Mediterranean Sea. The same holds for species native to tropical areas, with 14 species reported for the first time in the Mediterranean Sea, compared had six in the Northern Seas and two in the Bay of Biscay.

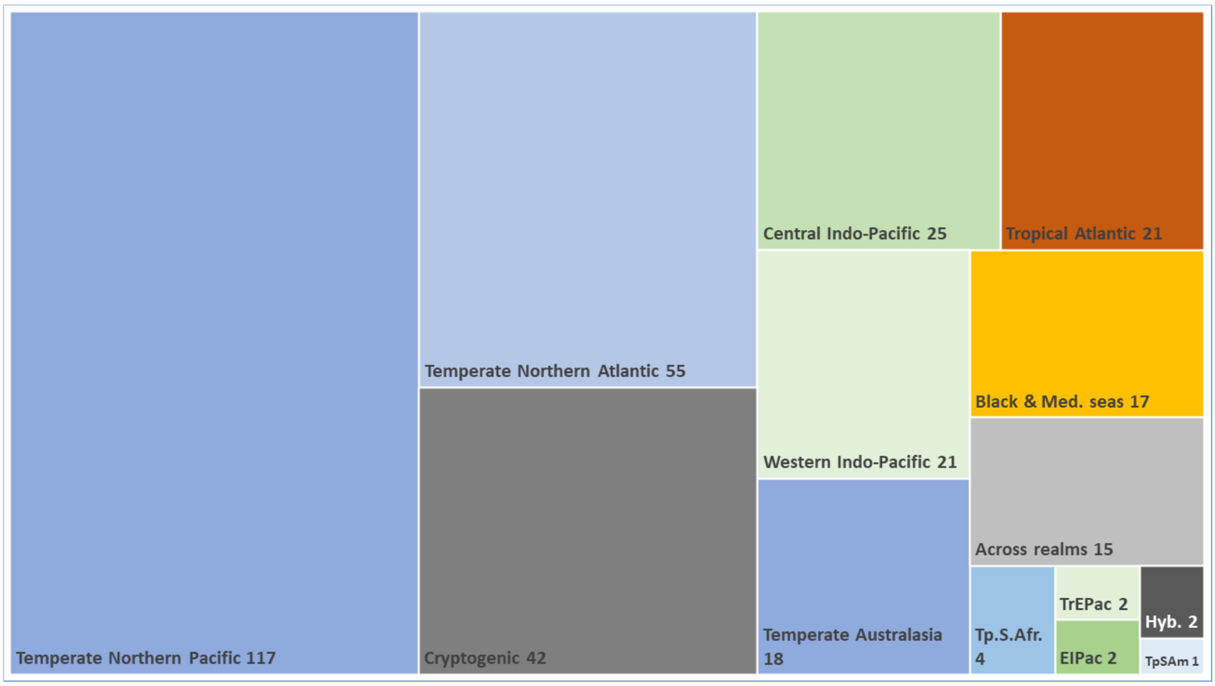


Figure 5. Origin (biogeographic realms) of the 342 marine NIS reported in Metropolitan France. "Across realms" stands for species with a native range spreading across several biogeographic realms (such as circumtropical species). Areas in small boxes, due to their limited contribution, have their names abbreviated as follows: "Tp.S.Afr.", "EIPac.", "Hyb.", "TrEPac" and "TpSAm" stand for Temperate Southern Africa, Eastern Indo-Pacific, Hybridisation (i.e., species resulting from a hybridisation between a NIS and a native species), Tropical Eastern Pacific and Temperate South America, respectively. Species in the group "Black & Med. Sea" are either native to the Mediterranean (*n* = 12), Black and/or Caspian Seas (*n* = 4), or both (*n* = 1).

3.4. Temporal Trends in Primary Detections

The number of new NIS reported (i.e., primary detections) was very low until the end of the 19th century, a time during which fewer than five newly introduced species were reported per decade (Figure 6). From the beginning of the 20th century until 1959, the rate of reporting of novel NIS or cryptogenic species was variable but never exceeded 11 species per decade (7 species per decade on average). Numbers slightly increased over the next decade (1960–1969; 17 species), whereas a surge in new NIS reports was observed at the start of the 1970s, with more than twice the number of new NIS reported from 1970–1979 (*n* = 48) as compared with the previous decade (Figure 6). Over the last five complete decades (1970 to 2019), on average, 49 arrivals were recorded per decade. During this period, most of the novel reports were made in the Mediterranean Sea, although the numbers between regions have been more balanced since the beginning of the 21st century, with a noticeable increase in numbers from the Northern Seas region (Figure 6).

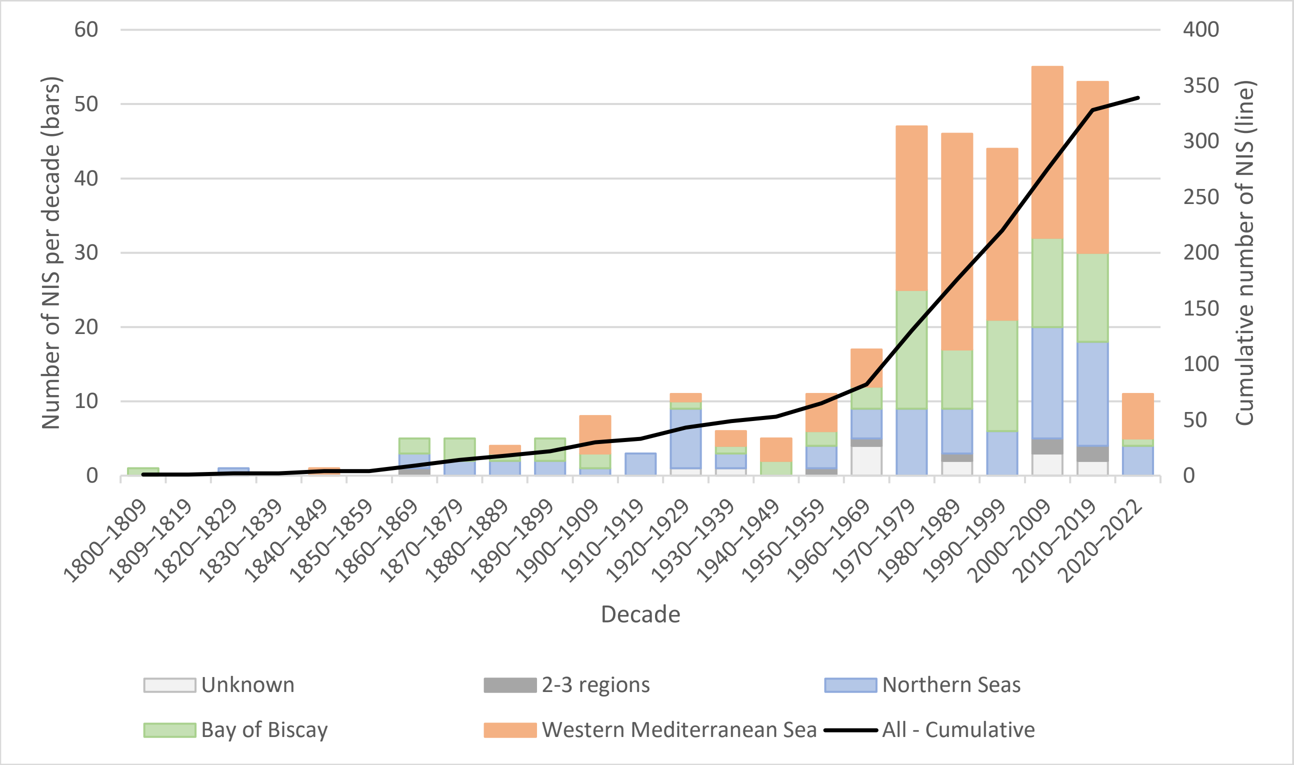


Figure 6. Number of new primary introductions per decade and region (bars, left vertical axis) and cumulative number for the three French regions over successive decades (line, right vertical axis). Bar colours indicate for each of the three regions a new NIS reporting in France. For 13 species, the region of first report is unknown, and eight species were simultaneously reported in more than one region (two or all three regions). Note that the last interval extends over three years only (2000–2022). The total number of NIS is 339, as three species were excluded because they corresponded either to a very old report (13th–14th century, *n* = 1) or had unknown (*n* = 2) dates for the first report.

4. Discussion

4.1. Update and Trends

Since the 13th century, 342 marine and estuarine NIS have been detected in French metropolitan waters. The majority (70%) of NIS is currently present in the Mediterranean Sea, which echoes the findings presented in studies at the European level [10,12,32]. This can be explained by the arrival of NIS through the Suez Canal, in addition to NIS introduced through other pathways, the main one being maritime traffic [33,34]. This list is a substantial update of all previously published ones for France, such as Goulletquer et al. [23], who focused on NIS from the open Atlantic French coast without the Mediterranean Sea, recording 96 NIS (excluding unicellular species). Compared with 2002, for the same geographic area (Bay of Biscay and Northern Seas), we found more than twice as many NIS, with 218 cryptogenic and NIS detected. Goulletquer [24] updated this list for the whole French coastline and found 276 NIS (excluding unicellular species). As compared with the list published in 2016, at a national scale, there was also an increase with 66 more NIS. According to our updated list, new NIS observations (since 2015) have been reported primarily in the Western Mediterranean Sea (47%), secondarily in the Northern Seas (37%) and in a lesser proportion in the Bay of Biscay (16%). These new NIS observations do not fully cover the difference of 62 species between the two studies. Some older observations were updated, such as for the cryptogenic species *Amphogona pusilla* Hartlaub, 1909, observed since 1964 or the non-indigenous annelid *Boccardiella hamata* (Webster, 1879) reported since 2010 in French waters.

Sixty-two per cent of primary introductions were reported after 1980, with a noticeable increase between 2000 and 2022 (35%, $n = 119$), as shown by the cumulative numbers of new records in Figure 6. This trend, started in the 1970s, fits very well with global trends documented by Jouffray et al. [35] for marine aquaculture production and shipping, which are two major introduction pathways in Europe (Figure 4) [16]. The increase observed since 2000 can also be attributed to an increased awareness of the consequences of NIS introductions by the scientific community and public authorities, as evidenced by the increased effort to observe NIS in various monitoring programmes since 2004 (RESOMAR, BenthOBS, WFD and MSFD implementations). Research projects targeting NIS have also increased, as shown by the funding sources cited in the literature, together with better consideration of this pressure in regulations. It should, however, be noted that many NIS observations are fortuitous as France still lacks an operational broad-scale monitoring programme targeting NIS [7]. Taxonomic impediments also lead to focusing on certain NIS phylum compared with others given the available expertise. Note that, as compared with previously published lists, some species have also gone extinct, such as the Rhodophyte *Laurencia brongniartii* J.Agardh, 1841, *Hypnea musciformis* (Wulfen) J.V. Lamouroux, 1813, *Tritia corniculum* (Olivi, 1792), and others were removed because of status uncertainties, permanently or pending clarification of their status (see below). Because of the particular geographical situation of the 5500 km of French coastline belonging to several marine biogeographic regions [11] and because of important maritime traffic, recreational boating and aquaculture activities, the number of NIS is high compared with neighbouring countries. Although we can expect their numbers to have also increased in recent years, there were 133 NIS, including unicellular species, listed as present along the Portuguese coast [36] and 90, including unicellular species, in British marine and brackish waters [37]. More globally, a European update of NIS in 2011 published national lists of both uni- and pluricellular NIS, ranging from 17 NIS in Slovenian waters to 266 NIS in Italian waters, with 253 NIS in Spain, the only other country with both Mediterranean and Atlantic coasts [12]. Only one-third ($n = 107$, with 21 species being in their natural range in one of the three regions; Figure 2) of the NIS reported along the French coasts is shared across its three biogeographic regions. This pattern is in accordance with that observed for total benthic invertebrates' communities, with the Mediterranean sheltering the highest number of exclusive species [14]. As with NIS, the Bay of Biscay and Northern Seas have more benthic species in common than these two regions do with the Western Mediterranean [14]. Nevertheless, regardless of the first region of observation, many NIS are nowadays present in the three regions (Figure 7).

Despite the high NIS number, only a few species so far appear to have major impacts on biodiversity and ecosystem functioning, with fewer than 2% of NIS considered invasive with proven consequences. However, there may be a lag between the introduction of a NIS, its first record, and its first visible impacts, if any [38,39]. Moreover, it is recognised that IAS ecological and economic consequences are insufficiently understood since they are not systematically assessed [40]. The most recent and significant invasion phenomenon in European French marine waters is that of the blue crab *Callinectes sapidus* Rathbun, 1896, in the Western Mediterranean Sea. Since 2017, the rapid population expansion and densification along the French Mediterranean coast [41] has caused significant disturbances. To date, consequences are mostly visible to professional fishing activities in coastal lagoons, but it is very likely that environmental consequences will be observed in the near future. Recently, the Western Mediterranean Sea was also impacted by the brown algae *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee and H.S. Kim 2009 and the Rhodobionta *Lophocladia lallemandii* (Montagne) F. Schmitz [42]. Between 2018 and 2020, *R. okamurae* rapidly expanded along the Mediterranean coast near Marseille, reaching very high densities covering up to 85% in several areas, where it overgrew native species [43].

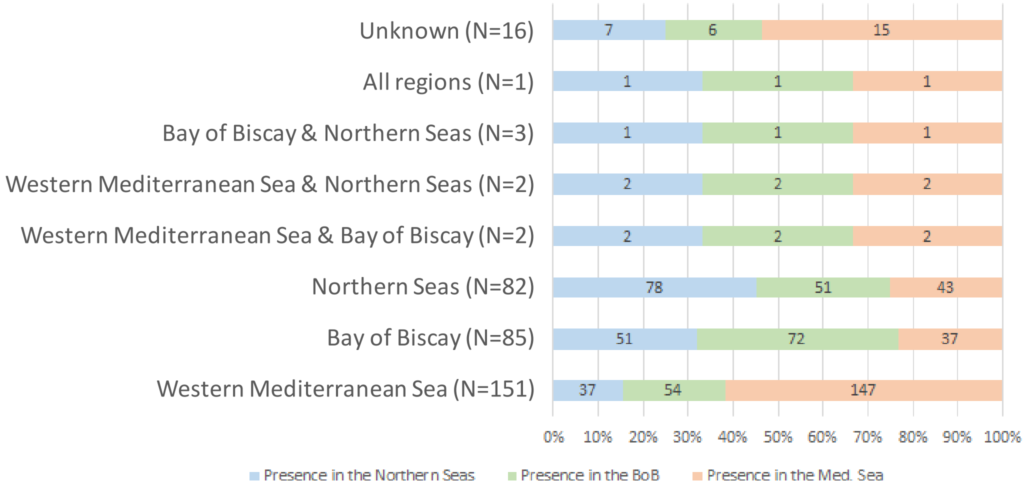


Figure 7. Number of NIS present in, and shared between, each French biogeographic region. For each region, N corresponds to the number of species first introduced in the considered biogeographic region(s). In each bar, numbers correspond to the number of species present in September 2022 in each biogeographic region. Note that the numbers include species present within their native range and introduced into another French region.

4.2. Vectors

Globally, trans-continental transport stowaways in ship fouling and ballast water are the main pathways of NIS introduction and expansion [2], and these pathways are likely to remain the most important, considering future increases of the global shipping network as forecasted by Sardain et al. [44] using socio-economic factors. These authors even concluded that increased global shipping trade could have a larger effect than climate-driven environmental changes on NIS introductions. It is thus critical to ensure a strong prevention of primary and secondary introductions by shipping. This requires a strict enforcement of current regulations, such as the Ballast Water Management Convention (IMO 2004) [45], and the development of novel regulations targeting fouling, which has until recently unfortunately been overlooked as a vector.

It is important, in terms of management recommendations, to make a clear distinction between (1) regular vectors over time, leading to routine introductions of NIS, with regular patterns of elimination and re-inoculation as shown for *Mnemiopsys leidyi* A. Agassiz, 1865 in the Bay of Seine [46], and (2) one-off "pulse" introduction events, some of which can be very broad-scale (e.g., the 2011 Japanese tsunami and subsequent transoceanic species dispersal, Carlton et al., 2017) and lead to secondary spread. The French oyster farming practices of the 1970s can be considered to be such a pulse event, placing transport as a hitchhiker on animals on top of the introduction vectors' list. Over 500 tonnes of the Pacific cupped oyster *Crassostrea gigas* (Thunberg, 1793), now named *Magallana gigas*, were imported from British Columbia, Canada (i.e., the temperate northern Pacific) for farming in the French Atlantic and Mediterranean. At the same time, over 10000 t of *M. gigas* spat were imported from Japan and Canada [47,48]. This voluntary introduction was accompanied by numerous involuntary NIS introductions, with, for example, fifteen NIS species having been observed following a collector's batch arrival in 1976 [15,49] in spite of management practices aimed to limit their survival. Following this important primary introduction, shellfish farming operations have regularly transferred *M. gigas* inside and across biogeographic regions and have thus been responsible for numerous secondary spreads across France and then Europe (see the main production areas in Figure 1). This could explain how part of the NIS introduced in one of the three regions are now present in the others (Figure 7). The fact that many aquaculture areas are adjacent to large ports makes it difficult to untangle the different pathways and retrace the primary or secondary vectors of introduction.

Although assessing the pathways of NIS introduction is vital for prioritising management, monitoring and surveillance activities [50], pathway assignments are often educated guesses because of a lack of certainty. Direct evidence and critical examination of concomitant possibilities are typically absent [2]. For many NIS, multiple introduction pathways are possible based on the multitude of human activities occurring in or near the locality of the first observation. Yet most of the time (64% in our study), only a single responsible pathway has been assigned or is considered as unknown. Polyvectism (sensu Carlton and Ruiz [51]) is certainly underestimated given the difficulty of acknowledging how and when an already established species was introduced. Moreover, a species' chances of successful establishment are also linked to propagule pressure (i.e., the number of introduced propagules, which can be larvae, spores, eggs, mature individuals, etc. and introduction frequency) [52,53]. These propagules may have been introduced through several vectors, as highlighted in the work of Williams et al. [54]. Genetic studies targeting marine NIS have documented very high propagule pressure and polyvectism [55,56] in relation to the life-history traits of many marine species (e.g., high fecundity, microscopic life stages and easily transported). In addition, it is likely that the percentage of multiple introductions (34%) has been strongly underestimated due to knowledge gaps in actual introduction pathways and vectors. Accounting for understudied pathways, such as the aquarium and bait trades, recreational boating and anthropogenic marine litter (e.g., [17,57–59]), could also lead to new insights and priorities for NIS monitoring and management.

4.3. Exclusions and Uncertainties about Species Numbers and Identification

As described in the methodology, the question of whether or not to include certain NIS arose. To help in decision-making, it is essential to define which species are concerned and which choices were made, for instance, excluding unicellular species. Some species were also excluded from our list because of important uncertainties regarding their identification. Moreover, this work highlights some points of caution, particularly regarding caveats either in terms of status (i.e., introduced or cryptogenic), origin or identification, which are detailed below.

Because the status of some phytoplanktonic species remains uncertain, the present study focuses on pluricellular eukaryotes, although unicellular NIS were recorded. For instance, the diatom *Coscinodiscus wailesii* Gran & Angst, 1931, was introduced in 1977 in the English Channel but its natural distribution range being in the Indian and Pacific Oceans. Its wide range of tolerance to environmental conditions and changes driven by global warming now allow this species to colonise the Atlantic coast of France, the United Kingdom (UK) coasts and the North Sea [60]. *Coscinodiscus wailesii* may lead to oxygen and nutrient depletion and subsequently impact mussel and seaweed production [61]. In benthic habitats, the Mediterranean benthic *Quinqueloculina carinatastriata* (Wiesner, 1923) and the Asiatic foraminifera *Ammonia confertitesta* Zheng, 1978, were recorded in the Marennes-Oléron Bay, in the Bay of Biscay, in 2004. Both were introduced from the Adriatic Sea [62] and in both the English Channel and the Mediterranean Sea [63,64], respectively. Benthic foraminifera play a key role in carbon cycling [65] and in fluxes at the sediment-water interface [66,67]; hence, the presence of NIS may disturb the equilibrium of benthic sediments, as suspected for the NIS benthic foraminifera *Nonionella* sp. T1 introduced in Scandinavian fjords [68]. Due to their small size, unicellular species are often excluded from NIS surveys. It is, however, important to track these invisible invaders, since their proliferation may impact ecosystem functioning through, for example, harmful algal blooms, and may potentially lead to public health issues. Another recent example is the presence of the toxic dinoflagellate *Ostreopsis* cf. *ovata* Fukuyo, 1981, in the French Basque coast (Bay of Biscay) since 2020, causing several human health issues, with about 700 people affected in 2021. According to Chomérat et al. [69], a possible introduction cannot be excluded.

The size and biogeographic diversity of the French coastline makes it essential to exercise caution with the construction and the use of the proposed national level NIS list. As an example, the nassariid gastropod *Tritia corniculum* is native to the Mediterranean Sea and its presence in the southern Bay of Biscay (Atlantic Ocean region) since 2008 is considered to be a range expansion. However, the presence of an individual found in 2013 in northern Brittany (Northern Seas region) was attributed to an aquaculture-related introduction [70]. The tale of this single species, with three different presence statuses across three biogeographic regions, demonstrates the nuance with which national lists should be viewed in EU countries spanning several regions. In addition, distribution ranges naturally change over time as a response to environmental changes over long time scales (e.g., glacial–interglacial cycles) or over shorter time scales (i.e., climate change) and should be considered in risk-assessment analyses (e.g., AS-ISK package [71]). The phenomenon of poleward spread is indeed well known and increasingly visible under current global warming [72]. This might make it more challenging to distinguish "true" species introductions (i.e., due to human-mediated transport) from natural spread. Such uncertainties are reported for *Tritia neritea*, a nassariid gastropod. Native to the Mediterranean and the Black Sea, as well as the Atlantic coasts of the southern Iberian Peninsula, its spread north to the Bay of Biscay in France in the 1970s–1980s has two possible (and not exclusive) explanations: climate warming or human-mediated introductions (such as a hitchhiker of farmed species, mainly oysters). The latter was supported by evidence, such as the habitat where the species was found (i.e., close to oyster farms [73]) and by genetic data. Genetic studies indeed revealed that the French Atlantic populations of this species showed a much higher genetic diversity than any native populations in the Mediterranean Sea and around the Iberian Peninsula. French Atlantic populations of *T. neritea* are composed of a mixture of several genetic lineages occurring only in specific locations in the native range and not at all found around the Iberian Peninsula. These two observations (proximity to oyster farms and higher genetic diversity) cannot be explained by a northward spread of the species from the Iberian Peninsula. The patterns observed supported a scenario of multiple-introductions from the native range, likely due to shellfish transfer from the Adriatic and Western Mediterranean Sea [74,75]. As shown with *T. neritea*, genetic studies can be helpful to validate the status (i.e., native vs. NIS) in different situations, but in many cases this approach has shown to be ineffective [76,77]. The ongoing environmental changes are likely to complicate potential updates of this work, making it difficult to discriminate between neonative sensu Essl et al. [72] (i.e., range expanding taxa tracking environmental changing) species and real NIS as defined in the introduction. Genetic studies can also be used to determine where a species came from. For instance, a phylogenetic analysis of mitochondrial COI gene sequences showed that specimens of *Polydora onagawaensis* Teramoto, Sato-Okoshi, Abe, Nishitani and Endo, 2013, collected from Normandy were grouped together with specimens from the USA into a single clade and were distinguished from the other three lineages comprised of Japanese and USA specimens, a result that casts doubt on the origin of this species in European waters [78].

More and more species are reported through citizen science initiatives, and, in particular, the reporting of colourful, new non-indigenous macrofaunal species, such as in the present list the records of the nudibranch *Polycerella emertoni* A.E. Verrill, 1880, the gastropod *Lamprohaminoea ovalis* (Pease, 1868) and the surgeonfish *Paranthurus hepatus* (Linnaeus, 1766). It is now recognised that citizen science plays an important role in monitoring NIS [79–81]. In addition to being a means of increasing awareness regarding NIS, the observations made by citizens can efficiently support monitoring programs for species that are easy to identify and are particularly helpful for documenting the occurrence range and expansion of previously reported NIS. Citizen science can indeed substantially increase the number and locations of observations that can be made. In a recent study assessing the potential of citizen sciences for seaweed surveys in the United Kingdom, the authors made several recommendations to increase the accuracy of citizen-science-based observations, including the use of georeferenced photos, training programmes with committed citizen scientists, identification resources, etc. [82]. However, even with these precautions, each observation must be checked by experts [83] on a case-by-case basis, especially when a NIS is first recorded. For example, the reporting of the tropical species *Hippocampus kuda* Bleeker, 1852, native of the Indo-Pacific region is questionable as it was reported only once in 2001 at the Grau du Roi (Western Mediterranean) by a diver while it has never been observed in the eastern Mediterranean Sea. Although the reality of this *H. kuda* observation, maybe released from a private aquarium, cannot be excluded, without scientific validation, this species was not added to the French list of NIS.

A large number of species require taxonomic expertise or even genetic analyses to be correctly identified. This is well exemplified by *Botrylloides diegensis* Ritter and Forsyth, 1917, and *B. violaceus* Oka, 1927, which are two important members of the fouling communities in marinas and ports in the English Channel in both the UK and France [84]. The two species were first reported based on colour morphs, following Lambert and Lambert [85]. *Botrylloides violaceus* has been described as showing single-coloured colonies (with diverse colours) whereas *B. diegensis* displays a distinctive two-coloured pattern (commonly orange against a dark background). However, molecular studies later showed that this trait, often used in field assessments or in citizen science programmes, can be misleading. Viard et al. [86] indeed reported that 59% of 627 single-colour colonies sampled in marinas of the English Channel and first assigned to *B. violaceus* were, in fact, *B. diegensis*. Interestingly, two-coloured and single-colour colonies of *B. diegensis* share the same mitochondrial COI haplotypes. In addition, these authors showed that single-colour *B. diegensis* colonies also exist in the Mediterranean Sea, including in Sète (France) near the Thau Lagoon, a well-known introduction hotspot. Differentiating with certainty the two species thus require a careful morphological examination (very rare for these taxonomic groups) and/or a genetic diagnostic; as a consequence, *B. diegensis* may have been strongly underestimated in previous surveys. Besides that, genetic analyses are required to correctly identify cryptic species (i.e., species that had been identified only with genetic markers, and for which diagnostic morphological traits have not yet been found) and recommended in the case of pseudo-cryptic species (i.e., cryptic species for which diagnostic morphological traits were finally identified but difficult to examine). In some cases, new NIS or cryptogenic species can be revealed in complexes of cryptic species. This is the case of the sea squirt *Didemnum pseudovexillum* Turon and Viard, 2020, a taxon newly described based on genetic evidence [87]. Colonies of the well-known invasive species *Didemnum vexillum* Kott, 2002, sampled in Brittany and Spain (Mediterranean Sea) were studied using nuclear and mitochondrial markers. The results pointed to a very divergent lineage and, thus, a putative cryptic species. The existence of this new species was further ascertained based on morphology: *D. vexillum* and the new cryptic lineage can be distinguished by several traits, notably spicule numbers [87]. For these reasons, the authors proposed a new species named *D. pseudovexillum* for its high morphological similarity with *D. vexillum*. The two species are found in ports and marinas, the English Channel and the Mediterranean Sea, thus two distinct biogeographic regions. Habitats and range led the authors to propose the introduced or cryptogenic status for the newly described species. Similar situations where both native and introduced/cryptogenic co-occur within a species complex lineage have been described in other colonial ascidians, such as *Botryllus schlosseri* (Pallas, 1766) by Bock et al. [39] or *D. vexillum* (excluding *D. pseudovexillum*) by Casso et al. [88], and are likely to be spread over numerous taxa in groups for which the taxonomic expertise is unfortunately declining.

Molecular tools (detailed below) are increasingly used to elucidate morphological identification uncertainties. As with *D. pseudovexillum*, this makes it possible to detect more and more new species misidentified so far and some of which actually are non-indigenous. The polychaete *Marphysa victori* Lavesque, Daffe, Bonifácio and Hutchings, 2017, has been misidentified as *Marphysa sanguinea* for decades; a molecular phylogeny study revealed it is actually a new species called *Marphysa victori* by Lavesque et al. [89], whose non-indigenous status and origin was unravelled a few years later [90]. Another interesting case study is polydorid species (Annelida, Spionidae), which inhabit the shells of the commercially important oyster *Magallana gigas.* Along the coast of Normandy (France) eight species, including five new NIS records for Normandy (*Polydora onagawaensis*, *Polydora websteri* Hartman in Loosanoff and Engle, 1943, *Boccardia pseudonatrix* Day, 1961, *Boccardia proboscidea* Hartman, 1940, and *Boccardiella hamata* (Webster, 1879)) and two first records in European waters (*P. onagawaensis* and *B. pseudonatrix*) were identified based on both morphological, genetic, and ecological characteristics [78].

These examples point to the absolute need to use an integrative taxonomic approach [91] with close collaboration between taxonomists and molecular evolutionary biologists. Such work is needed to ascertain species delineation and identification (i.e., barcoding studies based on properly identified voucher) within NIS monitoring programmes.

4.4. Available Tools to Limit this Invasion Phenomenon

Once established, it becomes almost impossible to eradicate or even regulate marine invasive NIS populations [92–94], especially if the species has significant effects on ecosystems [40]. Moreover, human activities causing introductions may continue to increase [44]. It is therefore essential to (1) implement management and biosecurity measures to limit introduction through anthropogenic activities; (2) predict as much as possible which species can be found where through risk assessments and modelling; and (3) detect introduced species as soon as possible thanks to innovative tools detailed below and implement a rapid response plan as defined in Reaser et al. [95].

Ojaveer et al. [96] recommend a multi-vector management approach to reduce the risk of NIS introduction and invasion. Eight years later, although this multi-vector management still does not exist, some measures have been taken internationally and nationally. Internationally, the International Maritime Organisations' Ballast Water Management Convention (BWMC) entered into force in 2017 with the objective to stop the introduction and spread of invasive species through ballast waters (IMO 2004) [45]. Under the BWMC, by September 2024 all ships must have installed a ballast water management system. In practice, port authorities have received little training in BWMC standards and compliance monitoring, leading to its weak enforcement [97]. In France, as presented in this work, the majority of NIS have been introduced as fouling species both through shipping or aquaculture activities through different pathways. Barring Council Regulation (EC) No 708/2007 of 11 June 2007 concerning the use of alien and locally absent species in aquaculture, which does not apply to certain species that were widely farmed before the regulation was written, such as *Magallana gigas* or *Ruditapes philippinarum* (A. Adams and Reeve, 1850), no international and national regulation of these pathways currently exists. Hull biofouling was only first discussed by the International Maritime Organization (IMO) in 2006. Although work is ongoing, as of yet there is no IMO convention addressing the issue of hull biofouling [98]. However, a French action plan to prevent the introduction and spread of IAS aims to block IAS (for a list of IAS of Union concern, see just below) outside the territory by 2030. According to Regulation (EU) 1143/2014 [99] on the prevention and management of the introduction and spread of IAS, Member States have (among other actions to implement) to take measures to stop the spread of the 88 invasive alien species of Union concern. Unfortunately, only 3 of these 88 are marine species: the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853, which spends only one phase of its life cycle in marine waters, the striped eel catfish *Plotosus lineatus* (Thunberg, 1787) and the brown algae *Rugulopteryx okamurae*. Adding further marine species in this list would imply that more measures should be taken to limit the introduction and spread of invasive marine NIS and thus limit consequences on biodiversity and ecosystems.

Modelling NIS introductions provides a decision support tool and allows the consideration of vectors [100], the risk of species spread [101–103], the risk analysis of species invasion [104–106] or the identification of introduction hotspots [107]. Because of France's geography, as shown here, some NIS species are present in only one of the three biogeographic regions (Northern Seas, Bay of Biscay and Western Mediterranean Sea). Invasion ecology predicts that the strongest impacts will likely be seen in recipient communities with high concentrations of specialist species [108,109] or in populations that are either small in size, low in genetic variability or already threatened by anthropogenic pressures [110]. Those communities with properties that confer high biotic resistance, such as high rates of predation or strong competitive interactions, are predicted to be the most resistant to impacts from invasive species [111]. Statistical and deterministic modelling approaches can be used to focus on the importance of three main components that lead to invasions: the introduction of propagules, the abiotic environment and biotic interactions [112]. Combined with risk assessment tools (i.e., Hawkins et al. [113]), it would be interesting to model the spread of those NIS present, for now, in only one of the three French biogeographic regions and use these joint approaches to anticipate where biological invasions are likely to be most problematic.

The third essential point to limit irreversible changes to ecosystems is early detection [114]. In this context, barcoding approaches have been used for a long time to either identify new species observed in the field or to confirm the identification of unknown specimens, which could be NIS [115]. This was, for example, the case for the ascidian *Asterocarpa humilis* (Heller, 1878), a newly introduced species for Europe, first detected in France and UK thanks to a genetic study [29]. We also provided above some examples (e.g., *B. diegensis*) for which the method was shown to be particularly effective to distinguish between two NIS that display similar external morphological features. DNA-based identification is, without a doubt, a powerful tool to lower uncertainties. However, in order to be accurate, this tool requires reliable reference sequences, which are still limited in taxonomic coverage for some groups of interest (i.e., which include numerous NIS and a strong decline in taxonomic expertise, such as bryozoans, hydrozoans or ascidians) [115]. Errors in databases, such as Genbank and even BOLD, are unfortunately commonplace (e.g., in *Botrylloides* sp., [86]). In addition, traditional barcoding approaches require processing each specimen one-by-one, making them both time-consuming and requiring substantial financial resources. Facing this limitation, high-throughput sequencing (HTS) has recently opened a new way to conduct NIS surveys and monitoring with the development of metabarcoding applied to environmental DNA or bulk DNA (for definition and scope, see Darling et al. [116]). Metabarcoding has been shown to be effective for NIS detection, including in ports and marinas, using DNA extracted from specimens collected on passive samplers (e.g., [117,118]), plankton samples (e.g., [119]), seawater [120] or a combination of different types of samples to increase NIS detection [121]. However, the interpretation of species lists delivered through metabarcoding must be carefully handled [116]. For instance, Couton et al. [120] showed that 17 out of 18 species obtained following metabarcoding all new and thus putative NIS for the study area were most likely false positives due to erroneous species assignment. In addition, the same authors showed that six NIS that were observed in the field at the time of the water sampling were not detected (i.e., false negatives) due to some technical limitations (e.g., amplification biases). This study and others outline the lack of maturity of molecular approaches and the need for further optimisation to be routinely implemented for marine NIS passive surveillance. Efforts are also still needed to increase standardisation of the approach [122]. It can however already be used for preliminary phases in setting up monitoring strategies or for regular surveys of some species for which there are reliable reference sequences and no technical risks of detection failure, thus for active monitoring programmes on a closed list of species. For instance, eDNA analyses were used to detect early invasion stages of the species *Mnemiopsis leidyi* in an economically important shellfishery region of UK [123]. As with every monitoring method, it is not devoid of limitations but, in view of the sound results obtained thus far in metabarcoding studies, its optimisation should be pursued. The approach indeed has many advantages, such as its cost-efficiency, ability to examine a large number of sites and capacity to be used at a high frequency, all of which are properties required for the rapid detection of new NIS. To another extent, the image analysis tools can be used in situ for species or taxonomic groups identification or colonisation processes [124], sometimes using artificial intelligence for the automated recognition of certain species in situ, when it is possible. Image analyses and video recording in labs were also successfully implemented to study the specific behaviour of non-indigenous species [125] and to study the predation of native species on NIS communities [126]. Early detection of species thanks to innovative tools allows species identification even during the lag phase and thus, as explained above, before potentially irreversible impacts. For greater efficiency against this pressure, early detection has to be associated with rapid communication of new observations and subsequent potential management measures, through collaboration between stakeholders.

5. Conclusions

The primary focus of this work is to provide an updated baseline inventory of NIS and associated data (taxonomy, origin, pathway of introduction, first record and status in French marine regions) for the metropolitan coasts of France. Uncertainties for some species are however highlighted. When uncertainty is related to taxonomic revisions, updating inventories becomes an absolute necessity. Some uncertainties can also be minimised through targeted monitoring, which uses appropriate complementary tools being fully aware of their advantages and limitations. Updating the status of each NIS with the geographical particularities of the three French marine regions raised the issue of administrative geographical boundaries, which are different from ecological marine regions. This can also create uncertainties about the species status in border areas and highlights the need for specific ecoregions reflecting species dynamics and habitat conditions. The statuses here reported may also be different in neighbouring states, as pointed out in Table 3 in Zenetos et al. (2022) [10] in which some species are native to one European country but introduced in another one. Lastly, the present work points to the large number of NIS in the Mediterranean Sea. It also highlights that, despite the specificities of the Western Mediterranean compared with the Atlantic coast (particularly warm waters), species introduced and still present in this region are able to establish in the two other marine regions. This phenomenon could be accentuated in future years due to global warming, coupled with increasing neonative (i.e., range expanding) species.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d15020161/s1, Figure S1: Number of NIS classified by taxonomic phyla at a national scale and for the three Frenchbiogeographic regions (Mediterranean Sea, Bay of Biscay and Northern Seas), Figure S2: Origin (biogeographic realms) of the 318 species for which the first introduction report was made in a single French region., Table S1: List of marine and estuarine non-indigenous species observed in the French metropolitan waters until September 2022.

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