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Review

Reviewing Introduction Histories, Pathways, Invasiveness, and Impact of Non-Indigenous Species in Danish Marine Waters

Kathe R. Jensen [1,*], Per Andersen [2], Nikolaj R. Andersen [3], Annette Bruhn [2], Helle Buur [3], Henrik Carl [1], Hans Jakobsen [3], Cornelia Jaspers [4], Kim Lundgreen [5], Ruth Nielsen [1], Beate Strandberg [6] and Peter A. U. Stæhr [3]

[1] Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark
[2] Department of Ecoscience, Section for Marine Ecology, Aarhus University, C.F. Møllers Allé 3, 8000 Aarhus C, Denmark
[3] Marine Biodiversity & Experimental Ecology, Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
[4] Centre for Gelatinous Plankton Ecology & Evolution, Technical University of Denmark, DTU Aqua, Kemitorvet 201, 2800 Kongens Lyngby, Denmark
[5] Lundsvænget 6, 5270 Odense N, Denmark
[6] Department of Ecoscience, Section for Terrestrial Ecology, Aarhus University, C.F. Møllers Allé 4, 8000 Aarhus C, Denmark
* Correspondence: krjensen@snm.ku.dk

Abstract: Non-indigenous species (NIS) are of concern for biodiversity conservation and ecosystem functioning. We present an updated list of NIS, including cryptogenic species, from Danish marine waters containing 123 species. Benthic invertebrates (36%) and phytoplankton (28%) dominate the list, but fish (15%) and macroalgae (13%) are also important. The Limfjord in Northern Jutland emerges as a hotspot for the introduction of NIS. Data from multiple sources were included, i.e., the National Monitoring Program (NOVANA), the National Fish Atlas project, the citizen science project Arter.dk, research articles, and annual national reports of the ICES working group ITMO. Forty-six NIS species were subject to expert judging using a modified Harmonia protocol; 19 were found to fulfil the four selected criteria identifying a species as being 'invasive'. Additionally, 38 species, not yet recorded in Danish waters, were evaluated using the same method, and 31 were found to fulfil the 'invasive' criteria. For nine selected species, introduction history, distribution maps, and time-series diagrams are presented. Our data document that the national monitoring efforts should be expanded to record macrozooplankton, coastal fish, and mobile epibenthic species. Furthermore, the national data repository, Arter.dk, should be expanded to enable more detailed documentation of new NIS records.

Keywords: marine invasives; problematic taxa; monitoring protocols; spatial coverage; temporal trends; impacts; expert evaluations; Marine Strategy Framework Directive

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1. Introduction

The introduction, spread, and establishment of non-indigenous species (NIS) in marine waters are one of the major threats to global marine biodiversity [1,2]. Future increasing anthropogenic maritime activities, such as shipping, offshore windfarms, and aquaculture, will increase the availability of vectors and stepping-stone substrates, which will likely accelerate the spread of NIS [3,4]. Increasing seawater temperatures with climate change will permit range extension by the secondary spread of NIS originally established in warmer waters, as well as the establishment of new introductions from warmer regions [5,6]. Most NIS have broad ecological and physiological tolerances and high reproductive potentials [7,8]. Most marine organisms have a planktonic stage during which propagules disperse according to prevailing currents. Hence, it is difficult to eradicate or even contain marine NIS once they are established in a new habitat [9].

All newly established NIS will somehow influence the local ecosystem, but in most cases, the impacts are minor and acceptable from a management point of view. A subset of marine NIS has demonstrated their potential to impose severe impacts on native species and cause reductions in ecosystem integrity, ecosystem services, human health-related effects, and/or cause tremendous socio-economic losses [10–13]. Management should be focused on preventing the introduction and spread of these so-called invasive alien species (IAS). However, predicting which species will become invasive and pose ecosystem impact risks remains challenging [14].

To address the risks NIS pose in European seas, the Marine Strategy Framework Directive (MSFD) requires EU Member States (MSs) to consider NIS in their marine management strategies [15]. Similarly, within the Regional Sea Conventions (RSCs) of OSPAR, HELCOM, and the Mediterranean, there is ongoing work to develop and refine indicators to assess NIS introduction and impact. For MSFD and RSCs, NIS is treated as a distinct descriptor (D2): "Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystem". A primary indicator (D2C1) addresses the rate of NIS introduction and two secondary indicators address the abundance and spatial distribution of established NIS (D2C2) and the impact of invasive NIS (D2C3) on species and habitats [16]. A recent account identified that 874 NIS had been introduced to European marine waters until 2020, with 250 NIS in the Greater North Sea, and with annual rates of new NIS introduction reaching 21 NIS per year^{-1} for the 2012 to 2017 assessment period [17].

The MSFD does not set standards for when a species can be considered to be invasive. The EU Regulation (1143/2014) on the prevention and management of the introduction and spread of invasive alien species [18] covers all ecosystems: marine as well as terrestrial and limnic. It defines invasive alien species as "alien species whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services". In Denmark, a standardized method for the evaluation of ecological, economic, and health impacts of invasive species was established in relation to the EU regulation on invasive species [19], and the guidelines for the assessment have recently been revised [20].

The objectives of the present study are: (i) to analyze an updated national list of NIS occurring in Danish waters and comment on some problematic species; (ii) to apply the modified Harmonia evaluation method to marine NIS occurring in Danish waters to produce a ranked list of invasive NIS. This method is also applied to species on a horizon-scan list; (iii) to present data on the spread and distribution of selected species from different functional groups and discuss the difficulties of obtaining such data for most marine NIS in Danish waters.

2. Materials and Methods

2.1. Study Area

Danish marine waters are located in the Northeast Atlantic and represent a transition zone from the high-saline North Sea to low-saline Baltic Sea waters. Salinity decreases gradually as water passes through the inner Danish waters via Skagerrak, Kattegat, through the Danish straits and the Belt Sea into the low saline central Baltic Sea. Danish waters are additionally characterized by a strong vertical stratification driven by density differences between low-saline Baltic waters at the surface and high-saline bottom waters at depth [21]. Vertical and horizontal salinity gradients have consequences for species richness and composition in both benthic and pelagic communities of Danish waters [22–24]. Most of the inner Danish waters are below 30 m in depth, and the bottom is primarily soft, sandy, and muddy sediments suitable for a range of infaunal species. Interspersed with these soft sediments are formations of boulder reefs, providing habitats for several sessile and mobile organisms of both algae and animals [24]. The boulders are interspersed with sand and gravel, providing habitats for both epi- and infauna species. Furthermore, Danish waters harbor more than 60 estuaries and coves, most of which are very shallow (<3 m), have short residence times, are dominated by seagrasses, and tend to be heavily loaded with nutrients [25]. Shipping is, furthermore, intense in Danish waters, with many industrial harbors providing artificial structures for NIS settlement [26].

Regional management areas overlap in the Danish transition zone with the North Sea, Skagerrak, the Limfjord, and Kattegat, covered by the OSPAR (Oslo-Paris) Convention, and the Baltic Sea, Belt Sea, Øresund, the Limfjord, and Kattegat covered by the HELCOM (Helsinki) Convention. It should be noted that the EU MSFD operates with a boundary in Øresund at the level of the bridge connecting Denmark and Sweden, whereas the OSPAR boundary is at the northern entrance to Øresund. ICES has already changed its ecoregional boundaries following the EU (https://www.ices.dk/data/Documents/Maps/ICES-Ecoregions.png (accessed on 19 December 2022), and it is expected that OSPAR will do the same in connection with the next Quality Status Report due in 2023.

For our analysis of non-indigenous species (NIS), Danish marine waters were subdivided into five sub-regions in agreement with [27]: (1) the North Sea and Skagerrak; (2) Kattegat; (3) the Limfjord; (4) the Belt Sea; and (5) the Baltic Sea, including most of Øresund (see Figure 1).

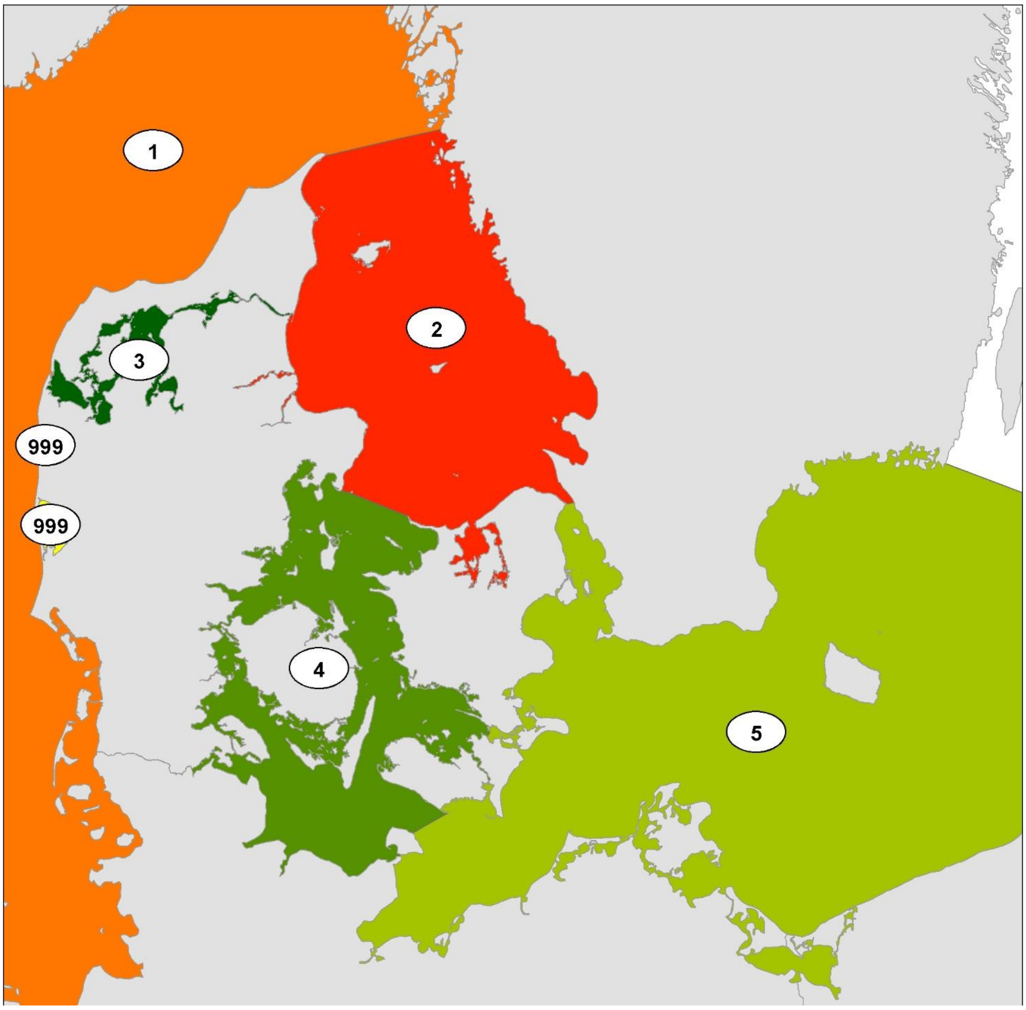

Figure 1. Map of Danish marine waters. Sub-regions are indicated in different colors: (1) the North Sea and Skagerrak; (2) Kattegat; (3) the Limfjord; (4) the Belt Sea; and (5) the Baltic Sea. The two areas labeled 999 are Nissum Fjord and Ringkøbing Fjord. Both have been included in sub-region 1 in this study.

2.2. Data Sources

In the present study, we analyzed data obtained by the Danish Environmental Protection Agency (EPA), from the Danish National Marine Monitoring Program (NOVANA), as well as records from published sources, including technical reports. Online databases such as AquaNIS, EASIN, AlgaeBase, WoRMS, and GBiF have also been consulted, as well as newly published scientific records within our expert community (this study, see supporting online material for records) and the Danish Fish Atlas project. Historical data are based on [28,29] and references therein. Some of the most recent introductions have been discovered through the citizen science project Arter.dk, where citizens, through an app or a website, can register species findings, which are then validated by an expert group (see https://om.arter.dk/videnbase/om-arter/om-arter/ (accessed on 19 December 2022)). Cryptogenic species have been included for precautionary reasons. Parasites have been included if data were available. In the text, the term NIS will, unless otherwise specified, refer to both non-indigenous and cryptogenic species.

We used the following functional groups for our study: phytoplankton, zooplankton, macroalgae and higher plants, benthic invertebrates, parasites, and fish. This is because collection, identification, monitoring, and assessment require different methods and expertise (see, e.g., [30–32]. Phytoplankton species have been included in this section for precautionary reasons, although for many of these species, their status as NIS is cryptogenic, or their appearance represents a climate-related expansion of their native ranges. The updated NIS list was analyzed for the year of first appearance of each species in Denmark and the subregion where it was first observed. A regression analysis of the accumulated number of NIS and the year of first observation was also performed. Finally, we attempted to analyze introduction pathways according to the Convention on Biological Diversity [33] categories, as far as this is known.

2.3. Expert-Based Scoring

The present authors have many years of experience working with marine NIS in several connections, e.g., national, EU, regional, ICES, and most have broad taxonomic expertise in one or more functional groups. Most authors participated in the expert assessment in connection with a consensus conference organized by the Danish EPA in November 2021. The evaluation follows the ISEIA guidelines [34] with slight modifications [20]. It includes expert judgements for each species based on the most recent data and knowledge on the six parameters: (i) dispersal; (ii) nature quality and conservation value of invaded habitats; (iii) impact on indigenous species; (iv) impact on the functioning of invaded ecosystems; (v) economic impacts; and (vi) health impacts. The experts assigned each of the six parameters a score between 0 and 3, where 0 is no impact, and 3 is a high impact, including a limited probability of recovery following eradication. The guidelines include more detailed descriptions of how to assign a certain score to each of the six parameters. For a species to be evaluated as invasive, the Danish EPA has set the following four criteria: the species shall reproduce and spread in the new habitat, i.e., the score for dispersal must not be 0. Additionally, the sum of the scores for both dispersal and nature quality of invaded habitats has to be $\geq$3; the species must have an impact on native species, i.e., the score for impact on native species must not be 0; and, in addition, the sum of scores for impacts on indigenous species and functioning of invaded ecosystems must also be $\geq$3 [20].

For the expert evaluations, two species lists were used: one comprising species already present in Danish waters (before 2021) and a horizon-scan list containing species that might be introduced into Danish waters within the next 10-year period.

For phytoplankton and, to some extent, zooplankton species, it is challenging to document anthropogenic activities as the cause of introduction. Except for the comb jelly, *Mnemiopsis leidyi* [21,35,36], very little scientific information is available to document the impacts on native species and ecosystem functioning, and hence, following the recommendations of the MSFD [37], these species were not scored for impacts [20].

2.4. Geographic Distribution over Time of Selected Species

The Danish National Monitoring Program, NOVANA, has monitored phytoplankton, benthic fauna, and macroalgae for about 40 years. Although NIS have not previously been specifically sampled, they can be identified retrospectively from earlier data. Based on available data and the results of the above analyses, we selected a few species representing the functional groups to show the distribution over time and space and the many different sources that need to be consulted to obtain data on spread and abundance, as suggested for MSFD secondary indicator D2C2. Two species of phytoplankton, *Pseudosolenia calcar-avis* and *Karenia mikimotoi*, were selected for the comprehensiveness of data; the macroalgae *Sargassum muticum* and *Gracilaria vermiculophylla* were selected for the different patterns of dispersal in Danish waters; and *Crepidula fornicata* was chosen for its long history in Danish waters. The round goby, *Neogobius melanostomus*, was selected as the only invasive fish; *Mnemiopsis leidyi* was selected for the large amount of research information on dispersal and impacts; and the two species of recently established species of *Hemigrapsus*, which are not presently represented in the NOVANA database, were selected to test the usefulness of the citizen science project Arter.dk. Maps and bar diagrams were based on available geo-referenced presence data (see Supplementary Table S2).

3. Results

3.1. Maintaining and Updating the List of NIS in Danish Waters

The Danish baseline list of marine NIS from 2012 contained 107 species, including 24 cryptogenic and 3 parasitic species. Of these, about 15, mostly fish that had escaped from aquaculture, had not established reproducing populations. The updated list (December 2021) comprised 123 species, plus one macroalga, *Chara connivens*, which occurs in freshwater in Denmark, but may have been observed in brackish water; this awaits verification (see Supplementary Table S1). Sources for the newly added species were research papers, technical reports, and "citizen science" records (see Supplementary Table S1). In the current gross list, we have listed phytoplankton species without determining their status as established or not established. Most species may form reproducing populations for several years and then disappear for several years to reappear unexpectedly. Almost all of the fish are freshwater species and are "not established" in marine waters, though some have been recorded numerous times after escaping from aquaculture facilities or private fishponds.

3.2. Problematic Taxa and Records

We have checked names and records in the baseline list and found some that had a wrong year of first observation, e.g., *Pachycordyle michaeli* listed as *P. navis* in 2012, and *Polydora cornuta*, which had been recorded many years earlier under a junior synonym, *P. ligni* and considered native by local specialists [38]. Rasmussen [39] listed records from Isefjord in 1943, and there are records from the Wadden Sea from the 1940s (1941–1947) [40]. As *P. ligni* has previously been confused with the native European *P. ciliata*, it is uncertain whether it might have arrived even earlier. WoRMS lists occurrences from the Mediterranean and the Black Sea as aliens, but not those from Ireland, Belgium, and France (https://www.marinespecies.org/aphia.php?p=taxdetails&id=131143#distributions (accessed on 3 January 2023)). Hence, its origin seems unclear, and we have changed the status to cryptogenic and the dates to 1941 and 1943 for OSPAR and HELCOM areas, respectively. *Polydora aggregata* has been tentatively identified from the port of Aarhus [41]. This is, so far, the only find outside its native West Atlantic distribution, and its identity needs confirmation.

Another polychaete, *Tharyx killariensis* was first reported in 2012 in Kattegat, and then identified as *Caulleriella killariensis* [27]. GBIF has 27 listings from Danish waters going back to 1996; these seem to originate from environmental reports from offshore oil and/or gas drilling in the Danish EEZ of the North Sea (https://www.gbif.org/occurrence/search?offset=0&country=DK&taxon_key=2324159 (accessed on 20 December 2022)). Furthermore, Kirkegaard [38] mentions *Caulleriella killariensis* from the northern North Sea, Skagerrak and Kattegat, and the species is not considered non-indigenous. It was initially described from Ireland [42], so if this species occurs in Danish waters, it is most likely a climate-related range extension rather than an anthropogenic transfer. Recent redescription of the species has shown that it is a species complex and that two newly described species of the genus are found in Kattegat [42]. A technical report surveying 16 Danish ports for NIS using both standard and eDNA methods found that the species found in the harbor of Esbjerg was similar, though not identical, to *T. robustus* Blake and Göransson, 2015, and may be an undescribed species [41]. The species in the Danish Wadden Sea has previously been described as *T. killariensis* or *T. marioni* [43]. The latter species is presently known as *Aphelochaeta marioni,* and this has been included in our list as a separate species (Supplementary Table S1). However, the identity of the species in the German Wadden Sea was recently recorded as *T. maryae* Blake and Göransson [44]. As there are apparently several cryptic species and different species may occur in the North Sea, the Limfjord and Kattegat, the correct identity and status as NIS of this species are uncertain.

The convoluted history of introducing *Marenzelleria* spp. to northern Europe is well known [45–47]. In the Baltic Sea, three species occur, the non-indigenous *M. viridis* and *M. neglecta* and the native *M. arctica* [46]. In Denmark, *M. viridis* was first described in Ringkøbing Fjord in 1990 [48]. More recently, it has been studied in Odense Fjord [49–51]. The species of *Marenzelleria* are difficult to distinguish without DNA sequencing [52], but *M. arctica* apparently does not occur in Danish waters. Whether *M. neglecta* occurs, and if so, when and where it first appeared, is uncertain. All specimens from Danish waters sequenced so far have been identified as *M. viridis*. Both *M. viridis* and *M. neglecta* have been recorded from Danish waters [53], but they do not give information on how the two species were identified. In the report by Andersen et al. [54], the authors did not identify either of the two species by eDNA methods.

For the hydroid *Pacycordyle michaeli*, the case is more complicated. It was recorded to have been present in Danish waters since 1935. This was a mistake. Rasmussen [39] misidentified this species as *Corydendrium dispar* Kramp, 1935, but Kramp's species is valid and occurs in deeper waters along the Swedish west coast [55]. The year 1935 was mentioned in the ICES WGITMO 2011 National Report for Denmark [56] (p. 77), and this has been transferred to the AquaNIS database and from there to other NIS lists. Schuchert [55] re-examined Rasmussen's material and identified it as the junior synonym *Pachycordyle navis*. The specimens reported by Rasmussen [39] had been collected in the Isefjord, in strong currents near the water intake to the power-plant Kyndbyværket in 1958. The occurrence near an artificial structure is interesting, since many other NIS occur in such habitats. As far as we know, the species has not been reported again from any localities in Danish waters, so it is unknown whether it is established or extinct.

Another problematic species is the shrimp *Palaemon elegans*, considered native to the North Sea, but introduced in the Baltic Sea. In Danish waters it has been well known from the North Sea through Kattegat and the Belt Sea to the Baltic Sea, at first under the synonym *P. squilla* (see Stephensen [57]) and later as *P. elegans* (see Rasmussen [39]). In the baseline list, the year of the first observation was listed as 1992. This is the first year it was recorded in the National Monitoring Program (NOVANA). Molecular studies have indicated that the population in the southern Baltic is different from that of the North Sea/northeastern Atlantic [58], and even newer studies indicate cryptic speciation of the species in the Mediterranean [59,60]. No such studies have included specimens from Danish waters, and we have included the species as cryptogenic, although it may be native throughout its Danish distribution.

Some of the species most recently discovered may still need verification of their identity. The amphipod *Grandidierella japonica* and the tanaid *Sinelobus vanhaareni* are probably correctly identified, but there is some doubt about the polychaetes *Hypereteone heteropoda* and *Streblospio benedicti*, and the red macroalga *Antithamnionella ternifolia*. *Hypereteone heteropoda* has not been found outside its native area in the northwestern Atlantic. *Streblospio benedicti* may be correctly identified, but its status as NIS is questionable; according to

WoRMS, it is considered alien in the Netherlands, but not in Belgium, France, and the UK (https://www.marinespecies.org/aphia.php?p=taxdetails&id=131191#distributions (accessed on 23 January 2023)). It was originally described from the east coast of North America. For the red alga *Antithamnionella ternifolia*, there are a few very similar species, both native and non-native. Apparently, voucher specimens have not been deposited, and photographic material of live specimens is unavailable.

3.3. Analyses of the Updated List of NIS in Danish Waters

The distribution of the species in functional groups is shown in Figure 2. Benthic invertebrates are the largest group of NIS, followed by phytoplankton. Fish and macroalgae are almost the same size. However, virtually all of the fish are occasional records of specimens escaped from aquaculture, whereas most of the macroalgae form established populations at least after a few years [61,62].

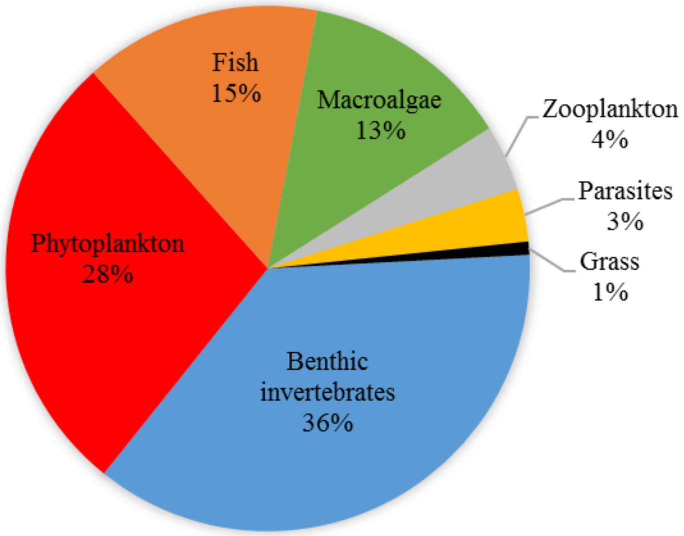

Figure 2. Distribution of functional groups of the 123 NIS recordings in Danish waters.

Based on the gross list from the Danish EPA (Supplementary Table S1), we have calculated the decadal accumulated number of NIS (including cryptogenic species) (Figure 3). The nine species introduced before 1900 have been merged into one bar. These species can probably be considered naturalized, except *Crassostrea virginica*, for which there are no recent records and can, therefore, be regarded as extinct, and *Cyprinus carpio*, which is not established in marine waters.

Most species occur in both OSPAR and HELCOM areas; ten species have not been recorded from the OSPAR region, and six species have not been recorded from the HELCOM region. When separated into sub-regions (Figure 4), the Limfjord stands out as a hotspot for NIS's arrival (or at least first detection) during the last four decades.

Figure 5′s top diagram shows the accumulated number of NIS per year. There is a drastic increase around 1980 (also visible in Figure 3), and linear regression analysis (Figure 5, bottom) resulted in significantly different slopes (introduction rates) of 0.44 NIS per year from 1900 to 1979 and 1.74 NIS per year from 1980 to 2020.

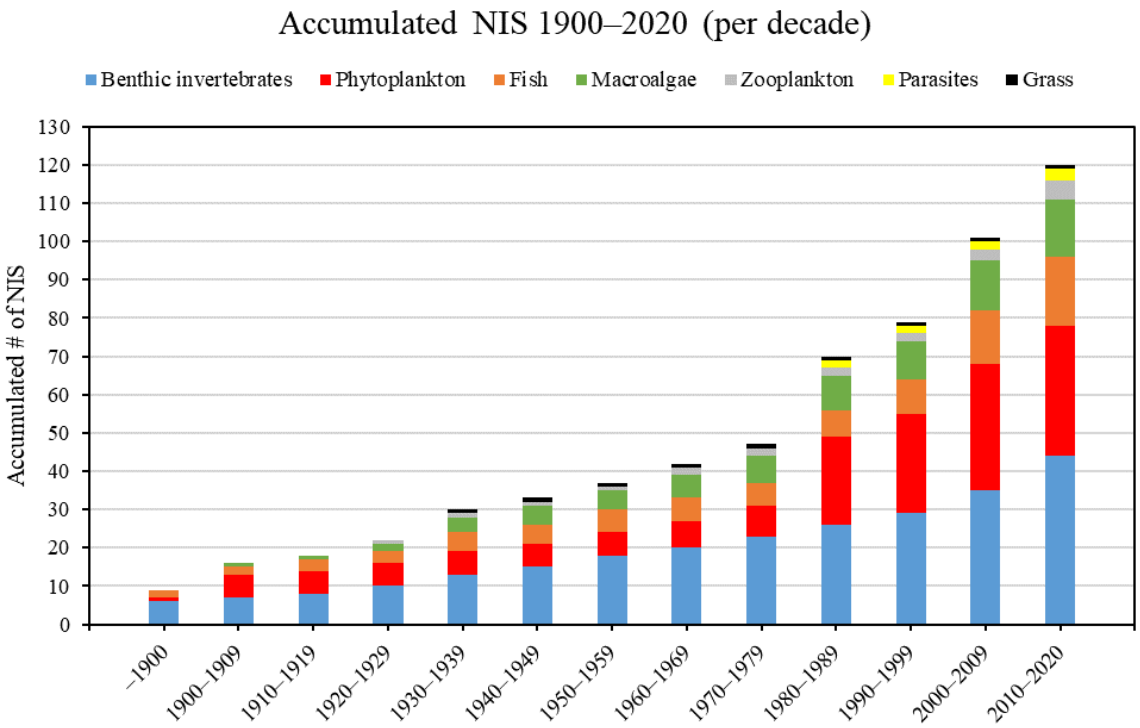

Figure 3. Accumulated number of NIS per decade. The nine NIS introductions recorded before the year 1900 are merged in the first bar: *Mya arenaria* (1245–1295), *Teredo navalis* (1853), *Platorchestia platensis* (1860), *Cyprinus carpio* (1879), *Amphibalanus improvisus* (1880), *Crassostrea virginica* (1880), *Cordylophora caspia* (1895), *Oncorhynchus mykiss* (1899), and *Prorocentrum triestinum* (1899). The three species first recorded in 2021 are not included.

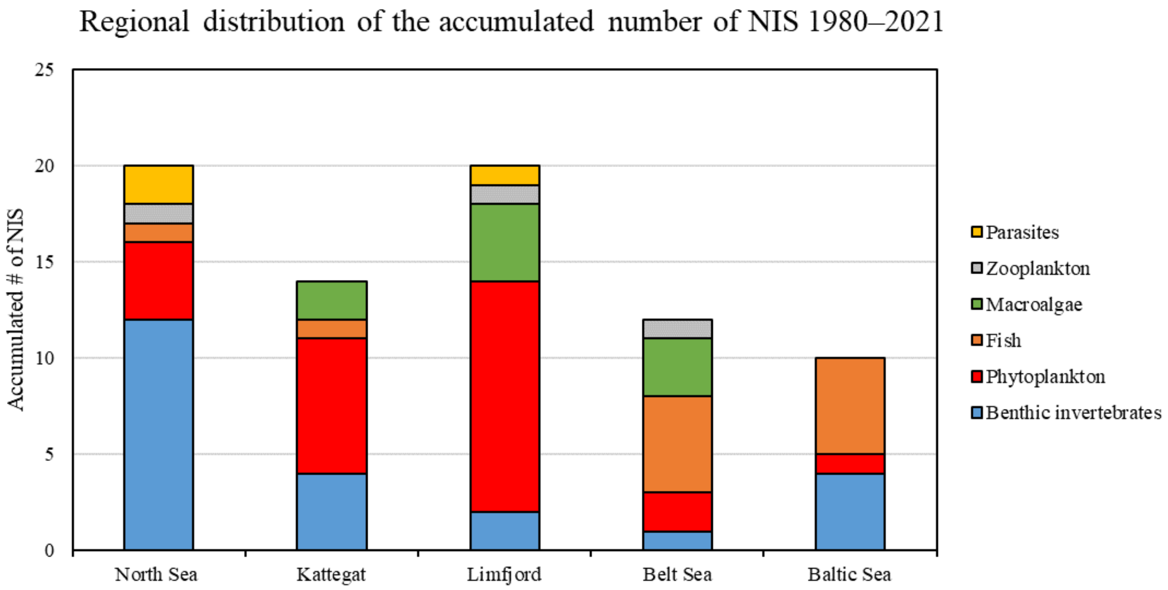

Figure 4. Sub-regional distribution of the accumulated number of NIS (first observations only) for the time period 1980–2021.

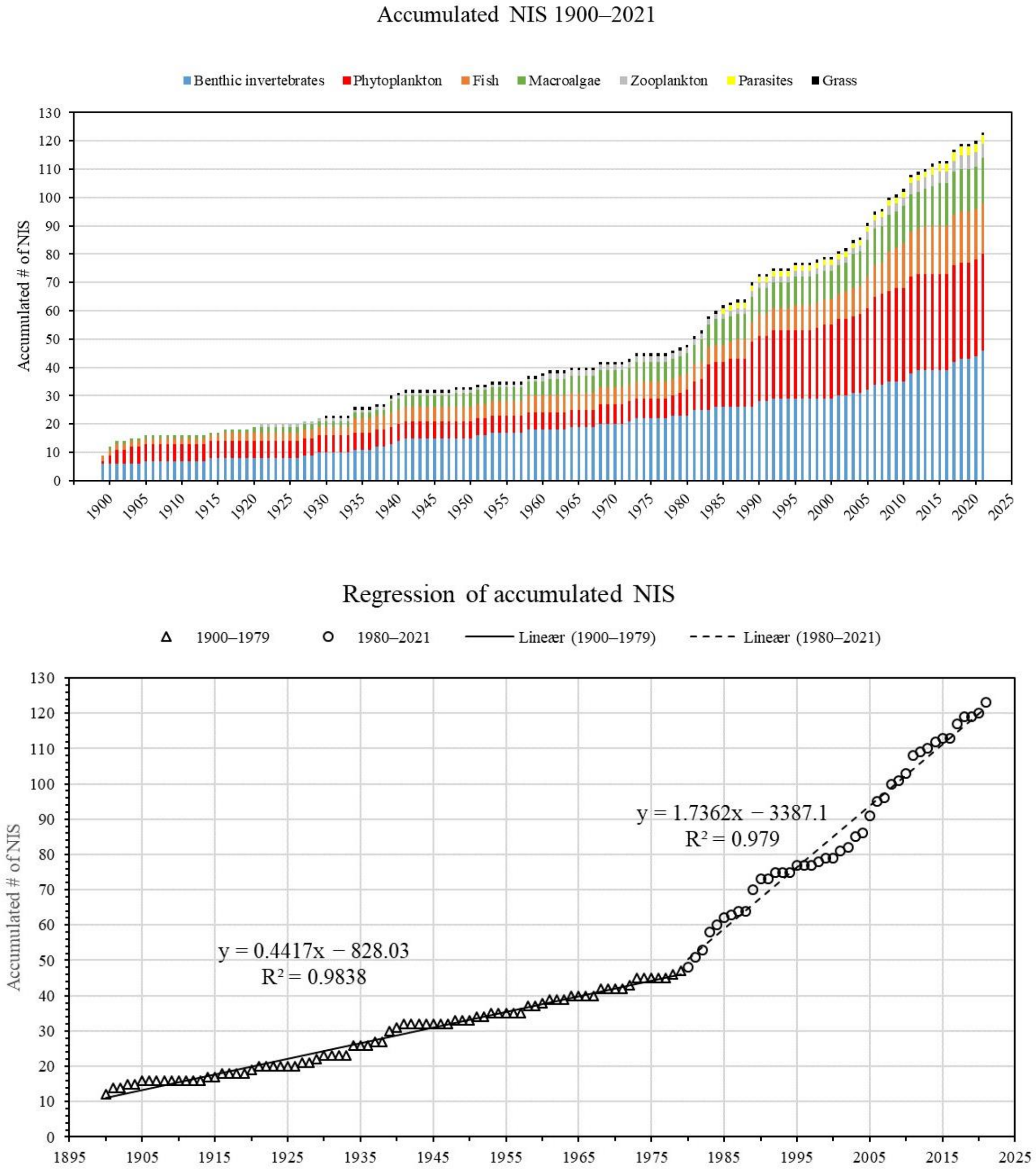

Figure 5. Top: the accumulated number of NIS divided into functional groups. **Bottom**: regression of accumulated number of NIS. There is a distinct increase in slope around 1980. The nine NIS recordings before 1900 are excluded from the regression analysis.

For each of the total 123 NIS introduction events, one or more categories of introduction pathways [33] have been reported. The percentage distribution of the different NIS introduction pathways is presented in Figure 6. More than 30% of the introduction pathways are reported as unknown. Of the known pathways, introduction by secondary introductions (natural spreading after introduction to a neighboring country) is the most dominant pathway, accounting for about 24%. Ballast water accounts for 23%, and aquaculture/mariculture for 11%. Hull fouling, sometimes merged with ballast water as a shipping pathway, accounts for 4%. Altogether, the remaining pathways (parasites on animals, contaminant on animals, contaminant nursery material, live food and live bait, other intentional release and fishery in the wild) account for about 6% of the introductions.

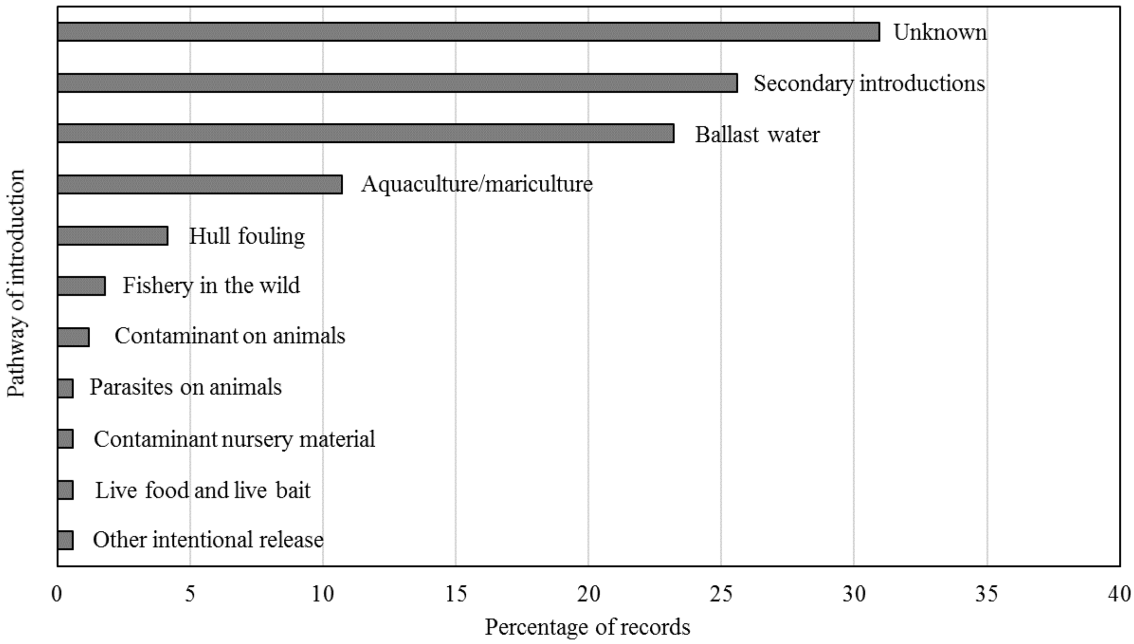

Figure 6. The percentage distribution of the different NIS introduction pathways. The categories of pathways of introduction are based on the CBD pathways categorization scheme [33].

3.4. Expert-Based Scoring

A total of 19 species fulfilled all four criteria for being invasive (Table 1). All species scored at least 1 for impacts on native species. Most species scored at least 1 for dispersal potential, except the hybrid *Spartina alterniflora x maritima* and most freshwater fish, which cannot reproduce in marine waters.

Table 1. Expert scores for marine NIS occurring in Danish waters. I—dispersal potential; II—conservation value of habitat; III—impact on native species; IV—impact on ecosystem functions; V—economic impacts; VI—health impacts. I and III must be >0 and I + II and III + IV must be ≥3. Scores fulfilling these criteria are in bold.

Species	**Functional Group**	**I**	**II**	**I + II**	**III**	**IV**	**III + IV**	**V**	**VI**	**Total Score**
Magallana gigas	Benthic invertebrate	**3**	3	**6**	**3**	3	**6**	2	2	**16**
Mnemiopsis leidyi	Zooplankton	**3**	3	**6**	**3**	3	**6**	2	0	**14**
Neogobius melanostomus	Fish	**3**	3	**6**	**3**	2	**5**	3	0	**14**
Sargassum muticum	Macroalga	**3**	3	**6**	**3**	3	**6**	2	0	**14**
Spartina anglica	Grass	**3**	3	**6**	**3**	3	**6**	2	0	**14**
Gracilaria vermiculophyllum	Macroalga	**3**	3	**6**	**3**	3	**6**	1	0	**13**
Ensis leei	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	2	0	**12**
Hemigrapsus sanguineus	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	1	0	**11**
Hemigrapsus takanoi	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	1	0	**11**
Styela clava	Benthic invertebrate	**2**	3	**5**	**3**	2	**5**	1	0	**11**
Marenzelleria neglecta	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	0	0	**10**
Marenzelleria viridis	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	0	0	**10**
Ficopomatus enigmaticus	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	1	0	**9**
Fucus distichus	Macroalga	**3**	3	**6**	**2**	1	**3**	0	0	**9**
Rhithropanopeus harrisii	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	1	0	**9**
Crepidula fornicata	Benthic invertebrate	**3**	2	**5**	**1**	2	**3**	0	0	**8**

Table 1. *Cont.*

Species	Functional Group	I	II	I + II	III	IV	III + IV	V	VI	Total Score
Ocinebrellus inornatus	Benthic invertebrate	**1**	2	**3**	**2**	1	**3**	1	1	**8**
Cordylophora caspia	Benthic invertebrate	**2**	2	**4**	**1**	2	**3**	1	0	**8**
Caprella mutica	Benthic invertebrate	**2**	2	**4**	**2**	1	**3**	0	0	**7**
Anguillicola crassus Kuwahara	Parasite	**1**	1	2	**3**	1	**4**	3	1	10
Pseudodactylogyrus anguillae	Parasite	**1**	1	2	**3**	1	**4**	3	1	10
Amphibalanus improvisus	Benthic invertebrate	**3**	3	**6**	**1**	1	2	1	0	9
Austrominius modestus	Benthic invertebrate	**3**	2	**5**	**1**	1	2	2	0	9
Colpomenia peregrina	Macroalga	**3**	3	**6**	**1**	1	2	1	0	9
Codium fragile ssp. *fragile*	Macroalga	**3**	3	**6**	**1**	1	2	1	0	9
Petricolaria pholadiformis	Benthic invertebrate	**2**	3	**5**	**1**	1	2	1	1	9
Teredo navalis	Benthic invertebrate	**2**	1	**3**	**1**	1	2	3	1	9
Bonnemaisonia hamifera	Macroalga	**3**	3	**6**	**1**	1	2	0	0	8
Dasya baillouviana	Macroalga	**3**	3	**6**	**1**	1	2	0	0	8
Dasysiphonia japonica	Macroalga	**3**	3	**6**	**1**	1	2	0	0	8
Dictyota dichotoma	Macroalga	**2**	3	**5**	**1**	1	2	1	0	8
Eriocheir sinensis	Benthic invertebrate	**3**	3	**6**	**1**	1	2	0	0	8
Melanothamnus harveyi	Macroalga	**3**	3	**6**	**1**	1	2	0	0	8
Mya arenaria	Benthic invertebrate	**3**	2	**5**	**1**	1	2	0	1	8
Mytilicola intestinalis	Parasite	**1**	1	2	**2**	1	**3**	2	1	8
Crassostrea virginica	Benthic invertebrate	**1**	1	2	**2**	1	**3**	1	1	7
Spartina alterniflora × *maritima*	Grass	0	3	**3**	**2**	2	**4**	0	0	7
Diadumene lineata	Benthic invertebrate	**2**	2	**4**	**1**	1	2	0	0	6
Gonionemus vertens	Zooplankton	**2**	2	**4**	**1**	1	2	0	0	6
Potamopyrgus antipodarum	Benthic invertebrate	**2**	2	**4**	**1**	1	2	0	0	6
Oncorhynchus gorbuscha	Fish	**1**	2	**3**	**1**	0	1	0	0	4
Oncorhynchus kisutch	Fish	**1**	2	**3**	**1**	0	1	0	0	4
Oncorhynchus mykiss	Fish	0	2	2	**1**	1	2	0	0	4
Salvelinus alpinus	Fish	0	3	**3**	**1**	0	1	0	0	4
Salvelinus fontinalis	Fish	0	2	2	**1**	1	2	0	0	4
Acipenser baerii	Fish	0	1	1	**1**	1	2	0	0	3
Acipenser gueldenstaedtii	Fish	0	1	1	**1**	1	2	0	0	3
Acipenser stellatus	Fish	0	1	1	**1**	0	1	0	0	2

The Pacific oyster *Magallana gigas* was not included in the original exercise because it is regulated under another EU Council Regulation on using alien species in aquaculture (EU Council Regulation 708/2007). However, we scored the species outside the expert assessment group with the highest score of all species (16). Furthermore, all scores would have had high or very high validity, i.e., they have been based on quantitative scientific information from Danish, Scandinavian, or North European populations [63–65]. There is no commercial culture of Pacific oysters in Danish waters, and commercial fishery is restricted. Handpicking is permitted, but difficult when dense reefs have been formed [66]. The species has now spread to most Danish waters, including Kattegat, the Belt Sea, and Øresund [63,66].

The second and third rank of invasiveness are the comb jelly, *Mnemiopsis leidyi*, and the round goby, *Neogobius melanostomus*, and recently a report on pressure factors in the marine environment [67] summarized knowledge about these two species as well as the Pacific oyster and number four on the list, the brown alga, *Sargassum muticum*, including comprehensive literature references. A more detailed assessment of *M. leidyi* and *N. melanostomus* was published later [68].

The two species of *Hemigrapsus* and the two species of *Marenzelleria* received identical scores for all parameters, and as they are difficult to distinguish, they have been merged when preparing fact sheets for use in management and citizen science projects.

Only one ascidian, *Styela clava*, was judged to be invasive. In fact, only two species of ascidians are considered NIS in Danish waters. None of the parasites scored high enough to be invasive. This is because their habitats (host species) cannot be considered of high conservation value, although the European eel is red-listed as critically endangered (FishBase: https://www.fishbase.se/summary/Anguilla-anguilla.html; accessed on 25 January 2023); the parasites do not cause this.

The Chinese mitten crab, *Eriocheir sinensis*, is on the EU list of invasive species of Union concern [69]. In our evaluation, it does not fulfil all the requirements for being invasive because it scores too low on impacts on ecosystem functions and also very low on impacts on native species. This is because few habitats are suitable for it to make the destructive burrows seen in our neighboring countries [70]. It is also uncertain if the species can be considered established, even though there are records of single specimens almost every year.

The American oyster, *Crassostrea virginica*, has been included in the NIS list, although it is almost certainly extinct from Danish waters. It did not score high enough to be considered invasive, mostly because it scored low on the conservation value of habitats. Attempts to culture the species in the 1880s in the western Baltic and southern Little Belt (which were actually under German supremacy at the time) were unsuccessful [71,72]. It is unknown if they failed due to cold winters or unsuitable habitats.

As mentioned in Materials and Methods, phytoplankton species were not scored according to the criteria used for the other species. Phytoplankton has the strongest reproductive potential of the groups considered in this study, and native as well as NIS species have seasonal lifeform patterns with periodical dominance. For NIS species with long-lasting blooms and significant impacts, it may be possible to quantify, and thus assess, these impacts. A good candidate for such an analysis could be the toxic dinoflagellate *Karenia mikimotoi*, which can form blooms lasting for months and reach extreme biomasses with density-dependent negative impacts at almost any level of the marine food web.

On the horizon-scan list, 31 species fulfilled all four criteria for being invasive (Table 2). Some of the species on this list have been found in Danish waters once or a few times, but do not appear to have established reproducing populations. Aside from the top five species on the list, it is impossible to rank the remaining species, of which most score 11, 10, or 9. The ascidian *Didemnum vexillum* has been found in several neighboring countries, e.g., the Netherlands [73], the United Kingdom [74], and, most recently, Norway (see https://www.museumstavanger.no/en/forskning/invaderende-sj\T1\opung-oppdaget-i-norge (accessed on 19 January 2023)). It is often associated with ports and marinas [74].

Table 2. Expert scores for horizon-scan marine species. *—these species have been found a few times, but are apparently not established. I—dispersal potential; II—conservation value of habitat; III—impact on native species; IV—impact on ecosystem functions; V—economic impacts; VI—health impacts. I and III must be >0, and I + II and III + IV must be ≥3. Scores fulfilling these criteria are in bold.

Species Name	**Functional Group**	**I**	**II**	**I + II**	**III**	**IV**	**III + IV**	**V**	**VI**	**Total Score**
Didemnum vexillum	Benthic invertebrate	**3**	3	**6**	**2**	3	**5**	2	2	**15**
Callinectes sapidus *	Benthic invertebrate	**2**	3	**5**	**3**	3	**6**	1	1	**13**
Potamocorbula amurensis	Benthic invertebrate	**3**	2	**5**	**2**	2	**4**	3	1	**13**
Undaria pinnatifida	Macroalga	**3**	3	**6**	**3**	3	**6**	1	0	**13**
Arcuatula senhousia	Benthic invertebrate	**3**	3	**6**	**2**	2	**4**	1	1	**12**
Charybdis (Charybdis) japonica	Benthic invertebrate	**3**	2	**5**	**2**	1	**3**	2	1	**11**
Paralithodes camtschaticus	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	2	1	**11**
Perna viridis	Benthic invertebrate	**2**	2	**4**	**1**	2	**3**	3	1	**11**
Homarus americanus *	Benthic invertebrate	**1**	2	**3**	**2**	2	**4**	2	1	**10**
Mulinia lateralis	Benthic invertebrate	**3**	2	**5**	**2**	1	**3**	1	1	**10**
Mytilopsis leucophaeata	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	1	1	**10**
Urosalpinx cinerea	Benthic invertebrate	**1**	2	**3**	**2**	1	**3**	3	1	**10**
Cancer irroratus	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	2	0	**10**
Gammarus tigrinus *	Benthic invertebrate	**2**	1	**3**	**3**	2	**5**	1	0	**9**
Dikerogammarus villosus	Benthic invertebrate	**1**	3	**4**	**3**	2	**5**	0	0	**9**
Obesogammarus crassus	Benthic invertebrate	**1**	3	**4**	**3**	2	**5**	0	0	**9**
Pontogammarus robustoides	Benthic invertebrate	**1**	3	**4**	**3**	2	**5**	0	0	**9**
Gmelinoides fasciatus	Benthic invertebrate	**1**	3	**4**	**3**	2	**5**	0	0	**9**
Celtodoryx ciocalyptoides	Benthic invertebrate	**2**	3	**5**	**2**	2	**4**	0	0	**9**
Chama pacifica	Benthic invertebrate	**3**	2	**5**	**2**	2	**4**	0	0	**9**
Palaemon macrodactylus	Benthic invertebrate	**3**	1	**4**	**2**	2	**4**	1	0	**9**
Rapana venosa	Benthic invertebrate	**1**	1	2	**2**	2	**4**	2	1	**9**
Schizoporella japonica *	Benthic invertebrate	**2**	2	**4**	**2**	2	**4**	1	0	**9**
Corbicula fluminalis	Benthic invertebrate	**2**	3	**5**	**2**	2	**4**	0	0	**9**
Procambarus acutus	Benthic invertebrate	**1**	3	**4**	**2**	2	**4**	1	0	**9**
Boccardia proboscidea	Benthic invertebrate	**2**	1	**3**	**2**	2	**4**	1	0	**8**
Cercopagis (Cercopagis) pengoi	Zooplankton	**2**	2	**4**	**2**	1	**3**	1	0	**8**
Bugula neritina	Benthic invertebrate	**3**	2	**5**	**1**	1	2	1	0	8
Pseudodiaptomus marinus *	Zooplankton	**2**	2	**4**	**2**	1	**3**	1	0	**8**
Cornigerius maeoticus	Zooplankton	**2**	2	**4**	**2**	1	**3**	1	0	**8**
Corella eumyota	Benthic invertebrate	**2**	1	**3**	**2**	1	**3**	1	0	**7**
Ruditapes philippinarum	Benthic invertebrate	**3**	2	**5**	**1**	1	2	1	0	8
Rangia cuneata	Benthic invertebrate	**2**	2	**4**	**1**	1	2	1	0	7
Amphibalanus amphitrite	Benthic invertebrate	**3**	1	**4**	**1**	1	2	1	0	7
Echinogammarus ischnus	Benthic invertebrate	**1**	3	**4**	**2**	1	**3**	0	0	**7**
Echinogammarus trichiatus	Benthic invertebrate	**1**	3	**4**	**2**	1	**3**	0	0	**7**
Hesperibalanus fallax	Benthic invertebrate	**1**	2	**3**	**1**	1	2	1	0	6
Beroe ovata *	Zooplankton	**3**	1	**4**	**1**	1	**2**	0	0	6

The bivalve *Potamocorbula amurensis* is a native of the northwestern Pacific. It has invaded San Fransisco Bay on the west coast of the USA [75]. However, this seems to be the only place outside its native area, and it must be considered unlikely to arrive and establish in Danish waters. The second bivalve of the top-ranking species, *Arcuatula senhousia* (previously known as *Musculista senhousia*), is also a native of the northwestern Pacific. However, this species has been found in several European countries, e.g., France [76], the Netherlands [77], and the United Kingdom [78].

The blue swimming crab, *Callinectes sapidus*, has been found twice in Danish waters [79], and the American lobster, *Homarus americanus*, was caught a single time in Øresund in January 2007, reported in Danish newspapers.

The ctenophore, *Beroe ovata*, was first found and identified by DNA sequencing in the Great Belt between December 2011 and January 2012 [80]. It has subsequently been identified in the Limfjord [81], but due to its narrow prey range is not expected to lead to large ecosystem impacts, but could potentially control *M. leidyi* abundances as suggested for the Black Sea invasion [82].

The planktonic copepod, *Pseudodiaptomus marinus*, was reported along the North Sea coast of northern Jutland [83], but this data was unavailable to us during the horizon-scan exercise.

For *Gammarus tigrinus*, there are only two records in the NOVANA database from Randers Fjord in May 1990. Rewicz et al. [84] found it at Bornholm in 2018, but there are no other records, whether in technical reports or citizen science projects, so it may have been established locally, but without obvious impacts at these localities. Like all amphipods, the species broods its young, and thus has a limited means for dispersal by its own means, despite having high fertility and a broad tolerance to environmental factors [85]. The species has spread along the southern coasts of the Baltic Sea since 1975, and reached the Gulf of Finland in 2003 [86].

Besides *G. tigrinus*, a number of amphipods, primarily of Ponto-Caspian origin, are on this list. They have all been found along the southern coasts of the Baltic Sea, and some have severely impacted native amphipod populations [87,88]. These species occur only at very low salinities, and even if they may be transferred to Danish waters, there will be few suitable habitats. However, some of these species are able to osmoregulate and may, therefore, be able to inhabit somewhat higher salinities [89].

The top-ranking macroalga is *Undaria pinnatifida*, which is number four on the list. It is native to the northwestern Pacific and has been introduced to several continents with oysters. The history of invasion in the marine environment in Europe was summarized by Schiller et al. [90], who also recorded the species from the German Wadden Sea, so it may soon be found in Danish waters as well.

No phytoplankton species were included in this part of the exercise. As has been stated earlier, it is very difficult to determine the native region of these species, and only for species with severe impacts and a likely native area will it be possible to judge their invasiveness.

3.5. Temporal and Spatial Distribution of Selected Species

To illustrate the variation in spatial distribution and changes in occurrences of species with different introduction and dispersal histories as well as a high impact score, we selected nine species representing key functional groups included in this study and for which data on distribution and occurrences were available. These include the macroalgae *Sargassum muticum* and *Gracilaria vermiculophylla,* which have been included in the National Monitoring Program (NOVANA) since their first observation in Danish waters. The slipper limpet, *Crepidula fornicata*, has a long history in Danish waters and has been found in the NOVANA program since marine monitoring was established around 1990. The two species of *Hemigrapsus* crabs are relatively new arrivals in Danish waters, and very few records are found in the NOVANA database. Most of the available data for these species are from the citizen science database Arter.dk. *Mnemiopsis leidyi* and *Neogobius melanostomus* are not included in the NOVANA program, but both have been objects of several research projects recording both distribution and abundance data. The phytoplankton species, *Karenia mikimotoi* and *Pseudosolenia calcar-avis*, are included in the NOVANA program. Below, we give a short presentation of each of the species.

Pseudosolenia calcar-avis (Schulze) Sundström, 1986, is a cylinder-shaped, up to 800-µm-long and 90-µm-diameter, planktonic diatom (Bacillariophyceae) with disputed taxonomic position. It was first described in 1858 by Schultze as *Rhizosolenia calcar-avis* and until recently, it was known under this name. However, a revision by Sundström pointed out that this species, contrary to other species of the genus *Rhizosolenia*, has curved terminal spines [91]. Sundström erected a new genus, *Pseudosolenia,* to house *Rhizosolenia calcar-avis* as *Pseudosolenia calcar-avis*. Unfortunately, most online databases (e.g., WoRMS, GBIF, AquaNIS) accept both names and even use different ID numbers and list different records under each name. It is beyond the scope of the present paper to try and sort out this nomenclatural problem, but AlgaeBase considers *Rhizosolenia calcar-avis* a synonym, and several recent research articles use the name *Pseudosolenia calcar-avis*, e.g., [92–94]. Hence, this will be the name used here.

The type locality for the species is in the German part of the North Sea, and it was first observed in Danish waters in 1898–1900 in the North Sea, Skagerrak, the Limfjord, and Kattegat [95]. After this, there are no records until 2009, after which it occurred regularly throughout Danish waters (Figure 7). This is surprising because intensive phytoplankton monitoring had already been active for more than 25 years [96]. The characteristic morphology of the species makes it unlikely that it has been overlooked, and it remains an enigma why it was absent for more than 100 years. Furthermore, it remains unknown whether anthropogenic activities have reintroduced the species.

In Danish waters, it spreads by surface currents. It does not do well in salinities below 12 psu. Hansen-Ostenfeld [95] considered it a typical autumn species (August–December), but it also occurred during May–July. In recent years it has occurred in late spring to late summer, with maximum concentrations in late summer, sometimes forming dense blooms in Kattegat, so possibly its physiological or ecological optima have changed.

On a global scale, the species has been recorded worldwide from tropical to cold-temperate seas (GBIF for *Pseudosolenia calcar-avis*: https://www.gbif.org/species/3194102 (accessed on 12 January 2023)). Its native region is unknown, and it should be considered cryptogenic.

A potentially adverse effect of *Pseudosolenia calcar-avis* is its capacity to outcompete other diatoms during the summer period. Furthermore, it is probably not grazed effectively by zooplankton due to its size and strong terminal spines. In the event of blooms of *Pseudosolenia calcar-avis,* it can potentially disrupt the flow of carbon in the food web. We hypothesize that it can hamper the pelagic food web structure, leaving a significant ungrazed quantity of the primary production to sink to the sea floor. To that end, blooms of *Pseudosolenia calcar-avis*, as with other diatoms, increase the risk of stress and increased mortality in fish in aquaculture. There is no indication that *Pseudosolenia calcar-avis* poses a health risk to humans.

Karenia mikimotoi (Miyake and Kominami ex Oda) Gert Hansen and Moestrup, 2000, is a marine, 20–40-µm, unarmored dinoflagellate (Dinophyceae). It is morphologically distinctive (Figure 8) and apparently easy to identify. In Lugol's fixed samples, the cells are seen as clover leaf-shaped cells. It was previously identified as *Gyrodinium aureolum,* originally described from the east coast of the USA. However, ultrastructural and molecular analyses identified specimens from Danish waters as *G. mikimotoi*, originally described from Japan, and further separated this and a few other species into a new genus, *Karenia* [97]. Yet, its position as a non-indigenous to North European waters has been questioned, although this was based on older literature with incomplete descriptions [98]. Given the general belief, with precautions in mind, we consider *Karenia mikimotoi* as a non-indigenous species in north European waters. *Gymnodinium nagasakiense* is considered a synonym of *K. mikimotoi*.

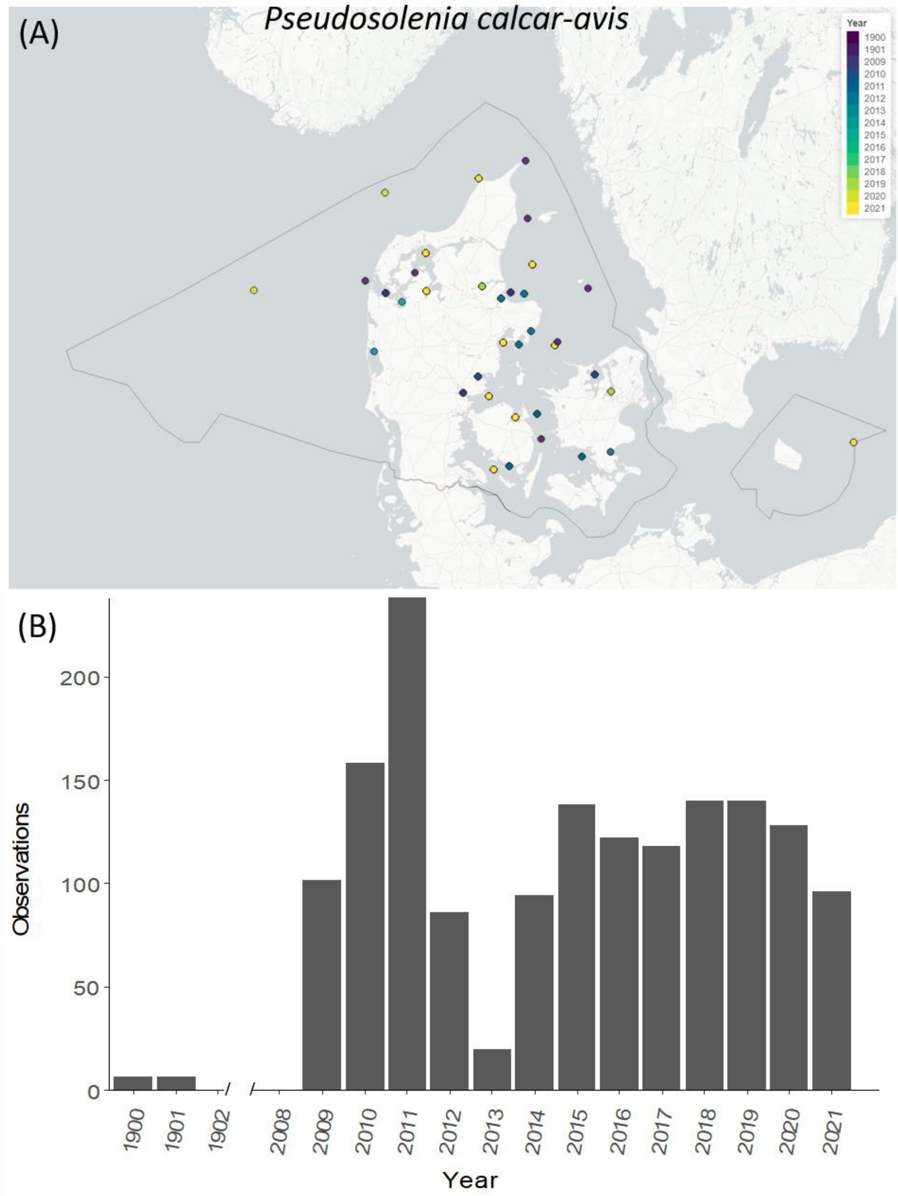

Figure 7. *Pseudosolenia calcar-avis*. (**A**) Map of sampling stations with known occurrences since 2009 within the Danish EEZ; (**B**) number of annual observations. Data from 2009 were obtained from the Danish National Monitoring Program (NOVANA) (Supplementary Table S2). Data from 1900 and 1901 are from [95].

It is considered mainly phototrophic, but there is some evidence of mixotrophic nutrition in laboratory settings.

The first report on *Karenia mikimotoi* in Danish waters is from 1968 [99]. It forms thin layer blooms in the pycnocline in the open North Sea [100] and dominates the phytoplankton community in the protected waters of the Limfjord. It is now well established with seasonal occurrences in Denmark (Figure 9).

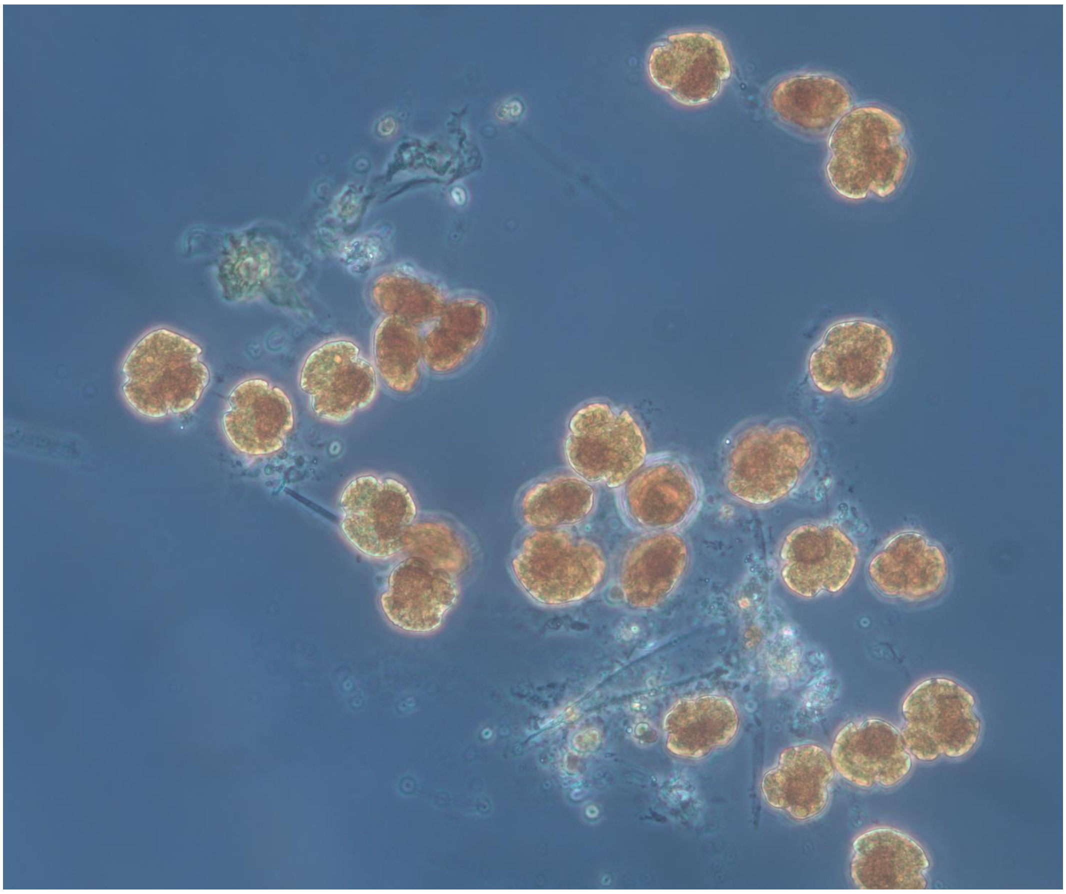

Figure 8. Light micrograph (phase-contrast) of cells of *Karenia mikimotoi*. Notice the clover leaf shape.

The genus *Karenia*, including *K. mikimotoi*, has been shown to be toxic to various groups of common microalgae in the marine environment [101]. In addition, suspected neurodegenerative effects on the development of fish larvae exposed to *K. mikimotoi* have been detected in laboratory studies [102]. The identification of a causative toxin is awaiting, yet dense blooms of *K. mikimotoi* have been claimed to be responsible for fish-kills in Norway and elsewhere, and at high concentrations, it causes mortality in rainbow trout under laboratory conditions [103,104]. Fish mortality might also be caused by gill irritations or decaying blooms of *Karenia mikimotoi* that sink to the seafloor, causing oxygen depletion and destruction of the benthic habitat.

Mnemiopsis leidyi A. Agassiz, 1865 (comb jelly), sea walnut. The sea walnut, *Mnemiopsis leidyi,* is a lobate ctenophore native to the east coast of the Americas. It has an oval body core with two lobes, eight comb rows, and four ciliated auricles next to the oral pole. The position of the aboral lobe insertion in relation to the statocyst is the key characteristic for the differentiation of the native *Bolinopsis infundibulum* from the non-indigenous *M. leidyi* (Figure 10). Animals go through a metamorphosis with eggs hatching into heart-shaped cydippid larvae that develop lobes and auricles during the transitional stage, while during the adult stage, tentacles are reduced, and the feeding mode changes. As adults, *M. leidyi* entrains large volumes of water due to current generation by the auricle [105], while larvae depend on a passive encounter of prey via fanned-out tentacles [106]. Larval and transitional stages are difficult to differentiate from other ctenophores.

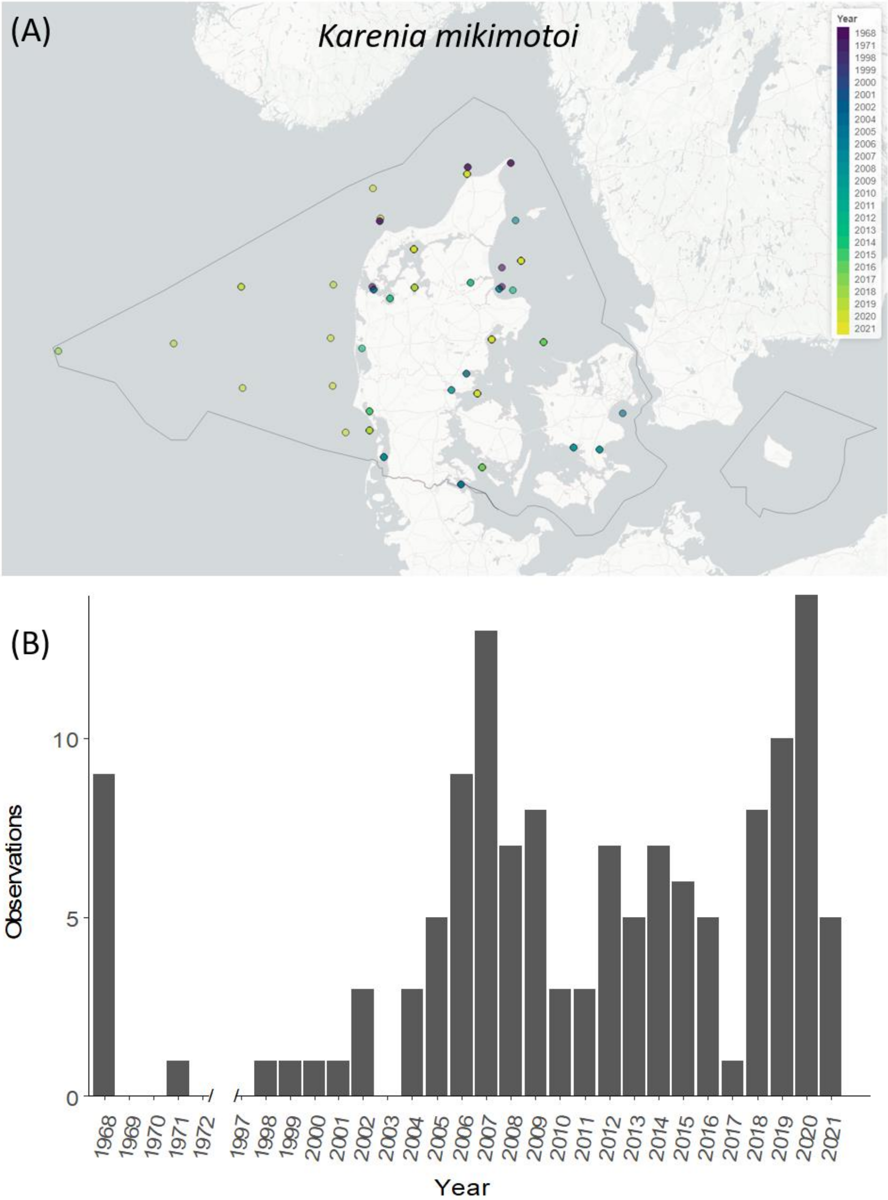

Figure 9. *Karenia mikimotoi*. (**A**) Map of sampling stations with known occurrences since 1998 within the Danish EEZ; (**B**) number of annual observations. Data from 1998 were obtained from the Danish National Monitoring Program (NOVANA) (Supplementary Table S2). Data from 1968 and 1971 from [99].

Mnemiopsis leidyi was first sighted in the early 1980s in the Black Sea and has subsequently spread throughout south-western Eurasia, including the Caspian Sea, Sea of Azov, Eastern Mediterranean Sea, and has most lately expanded into the NW Mediterranean Sea (as reviewed in [36]). In Northern Europe, *M. leidyi* was first officially confirmed in 2005 from different regions around the extended North Sea area, including the coast of the Netherlands during July [77], the Nissum Fjord in Denmark during August [107], Le Havre, the French part of the English Channel, during September [108], and the Oslo Fjord, SE Norway, during October [109]. By 2007, *M. leidyi* was confirmed in all Danish waters, including the Bornholm Basin (as reviewed in [36]). It is important to note that even though *M. leidyi* has a large tolerance towards environmental stressors, such as temperature and oxygen conditions (as reviewed in Jaspers, Bezio, and Hinrichsen [21]), salinity drastically impacts reproduction rates, and at low salinities, reproduction ceases [110]. This likely explains the lack of *M. leidyi* occurring further into the low-saline Baltic Sea than the Bornholm

Basin [111]. Furthermore, a short cold winter period (January–March) during the early 2010s led to the disappearance of *M. leidyi* from large areas of NW Europe, including the Baltic Sea, Belt Sea, Skagerrak/Kattegat, and Norwegian coastline from summer 2011 until spring 2014 [36]. However, one warm winter (January–March) with high current velocities during 2014 was sufficient for re-colonizing the entire distribution range occupied before 2011 (Figure 11). Further, no population structure was observed in the entire NW European distribution range in 2014. This indicates that the North Sea, where *M. leidyi* has been observed since its first recordings in 2005, acts as a refuge to swiftly re-seed animals over all Danish waters [36]. In this study, we include a presence/absence dataset from an extensive monitoring effort conducted in 2020, indicating the widespread distribution per previously published distribution maps [36]. It is important to highlight that certain regions, such as the Limfjord and coastal areas in the Kattegat and Belt Sea, can be regarded as abundance hot spots, where densities between 0.5 and 1 individuals L^{-1} have been documented (as reviewed in [36]).

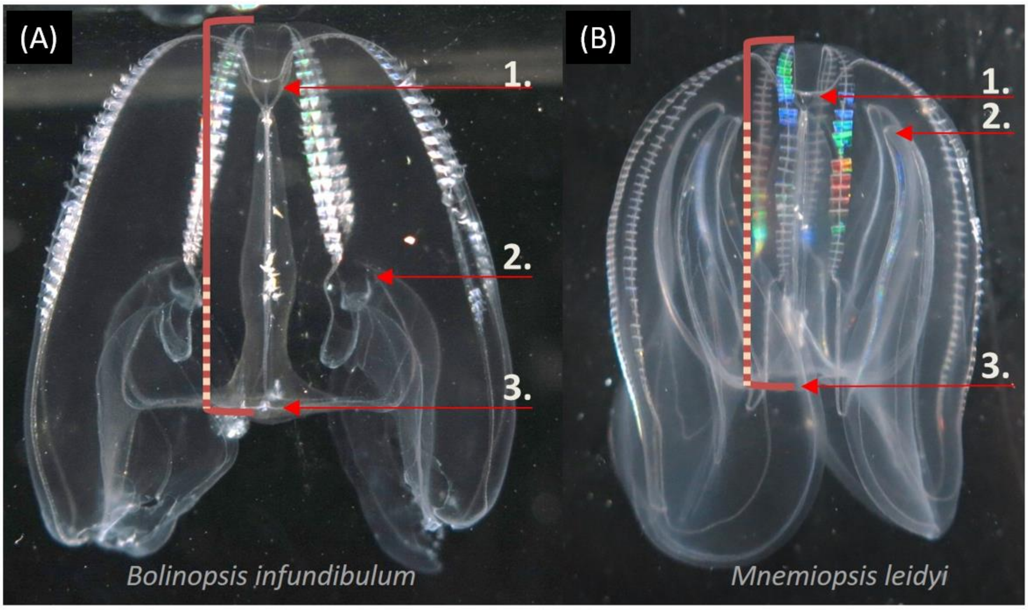

Figure 10. Characteristics of lobate ctenophores present in northern Europe with (**A**) the native *Bolinopsis infundibulum* and (**B**) the non-indigenous *Mnemiopsis leidyi*. Morphological differentiation is based on the position of the statocyst: (1) in relation to the insertion of the lobes (2) and the mouth; (3) in *B. infundibulum*, the distance between insertion of the lobes (2) and mouth (3) is about one-third of the oral-aboral length (red bracket), while it is two-thirds in *M. leidyi,* as indicated by the dashed line. Image credit: C. Jaspers, Kiel Fjord January 2015.

Due to the change in morphology, larvae and adult *M. leidyi* have different prey preferences. While adults primarily prey on larger zooplankton, such as copepods [105], larvae feed on microzooplankton <100 µm [106]. Reproduction rates are high, and in the Kattegat, it has been shown that one animal can produce up to 11,232 eggs per day, with carbon-specific egg production rates of 8.4 ± 1.4% of body carbon per day being channeled into reproduction for the largest-sized animals [112]. It is striking that this simultaneous hermaphrodite, which has a high hatching success during self-fertilization of 65–90%, keeps reproducing under starvation and channels energy from the body into gonadal tissue [113]. In fact, large-sized animals have been documented to keep reproducing for 12 days without food while shrinking in body size [113]. Due to a different prey size preference of larvae, this trait is expected to lead to a competitive advantage over other zooplanktivorous native species. It likely explains the fast population increase, especially in eutrophic areas, such as the Limfjord [114] or the Dutch Wadden Sea (as cited in [36]).

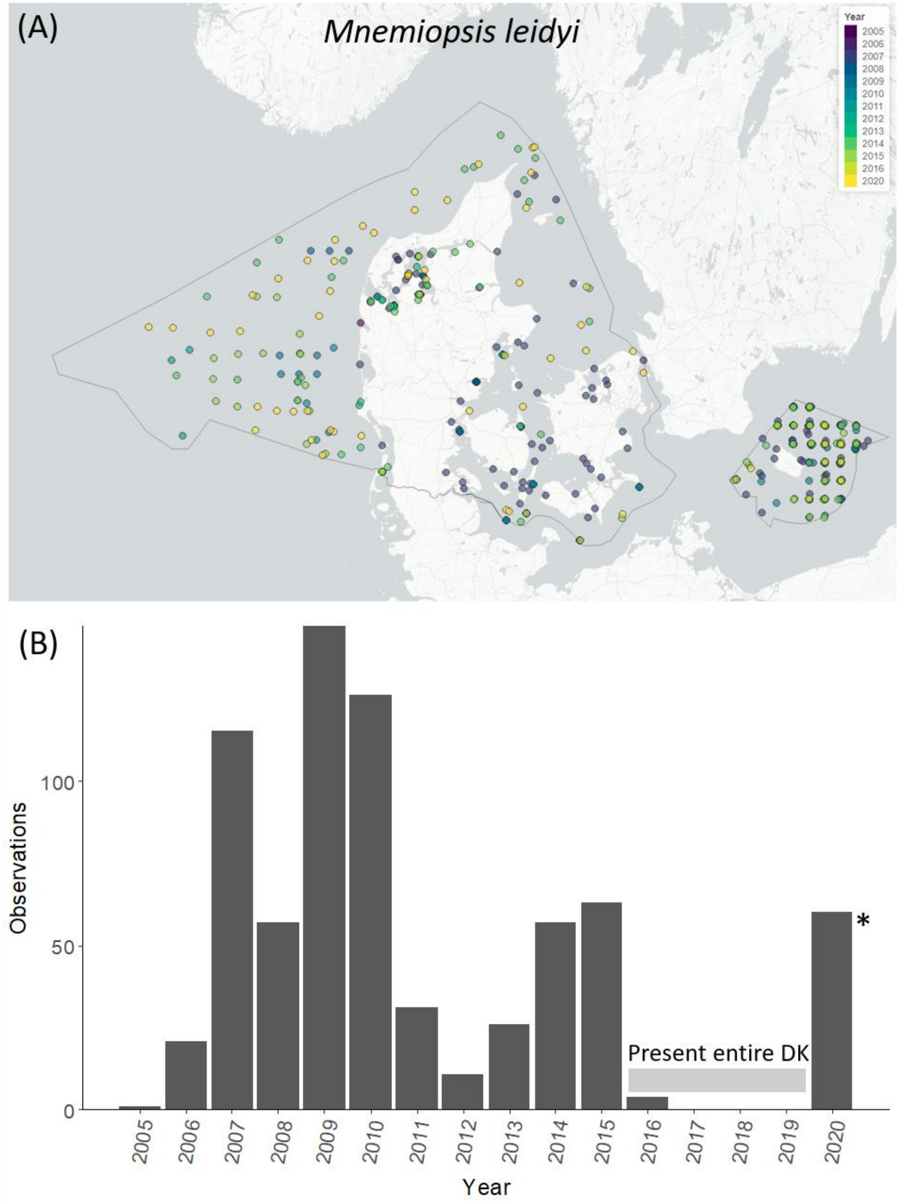

Figure 11. *Mnemiopsis leidyi* distribution pattern in Danish waters sorted by year (**A**) and cumulative yearly sightings (**B**). Note: time series of *M. leidyi* does not include observations for Danish waters from 2016 to 2019, when *M. leidyi* has been confirmed present across all Danish waters (C. Jaspers pers comment). * Bornholm Basin, with 45 station grids, sampled during March and November 2020, is not included.

Mnemiopsis leidyi shows a strong seasonality, which has the highest abundance during summer and autumn [111]. Salinity ranges govern details about its seasonal abundance peak [36]. Animals are present in Skagerrak/Kattegat areas from July to March and in the lower saline areas of the Belt Sea and Bornholm Basin from September to February [111], while *M. leidyi* larvae have been confirmed with molecular species verification to be present even when adults are absent [115]. This highlights the potential role of larvae to overwinter and seed the next year's generation, even though this hypothesis needs further investigation.

In areas where *M. leidyi* is very abundant, heavy predation control on the zooplankton has been documented, such as in the Limfjord [68,114] or in the Kattegat, where a cascading effect on copepods and diatoms has been documented in years where *M. leidyi* was present [35].

Especially for gelatinous zooplankton, we advocate for confirming the arrival of NIS with molecular tools to avoid confusing NIS with native species that have been disregarded in monitoring initiatives [116]. For example, the native ctenophore *Mertensia ovum* was mistakenly identified as *Mnemiopsis leidyi* in the northern Baltic Sea, but molecular analysis confirmed that this was a misidentification [116].

Crepidula fornicata (Linnaeus, 1758), slipper limpet. The slipper limpet, *Crepidula fornicata*, is a native snail of the northwest Atlantic from the Gulf of St. Lawrence in the north to the Gulf of Mexico in the south. It has a cap-shaped, oval shell with an almost invisible spire on the posterior right side. Internally, a characteristic calcareous plate forms a shelf supporting the visceral mass, and the foot covers the lower side. There is no operculum. The shell is up to 6 cm long, and pale yellowish with reddish or brownish dots or streaks (Figure 12). Slipper limpets occur on hard substrates, often the shells of other mollusks. They may form stacks of 4–6 individuals, of which the bottom individuals are females, and the top ones are males; hermaphroditic individuals may be located in the middle. Slipper limpets are suspension feeders, forming a mucus net to trap plankton and detritus particles [117].

Figure 12. *Crepidula fornicata* forming a stack of three individuals on the shell of a whelk, *Buccinum undatum*. Specimens were collected at low tide at Rømø, Wadden Sea in September 2007. Photo: K.R. Jensen.

Crepidula fornicata was first introduced to Europe with American oysters, *Crassostrea virginica*, and transferred to southern England between 1870 and 1890. It was subsequently transferred to the Netherlands, either with oyster spat, on hulls of ships, or as larvae in ballast water [117]. The first individuals found in Danish waters were reported in 1934 from Nissum Bredning in the western part of the Limfjord. They had apparently been transferred with young oysters from the Netherlands [118]. In the same year, German scientists found the species near Rømø in the Wadden Sea [119]. The first empty shells were recorded from Rømø in 1942, and in 1949 it was also found in the northern Kattegat [120]. Until recently, they had not been found south of the north coast of Djursland (western Kattegat) [28]. The NOVANA Monitoring Program has 519 records (Figure 13). The first records south of Djursland are from deeper water in Kattegat in 1992 and 1995. A total of 48 records are south of Djursland; the southernmost are from 2015 in Nakskov Fjord in the Baltic Sea. Most of the records south of Djursland are from 2011 to 2020, indicating a range expansion. Arter.dk has 100 records, but they do not distinguish between dead shells and live specimens.

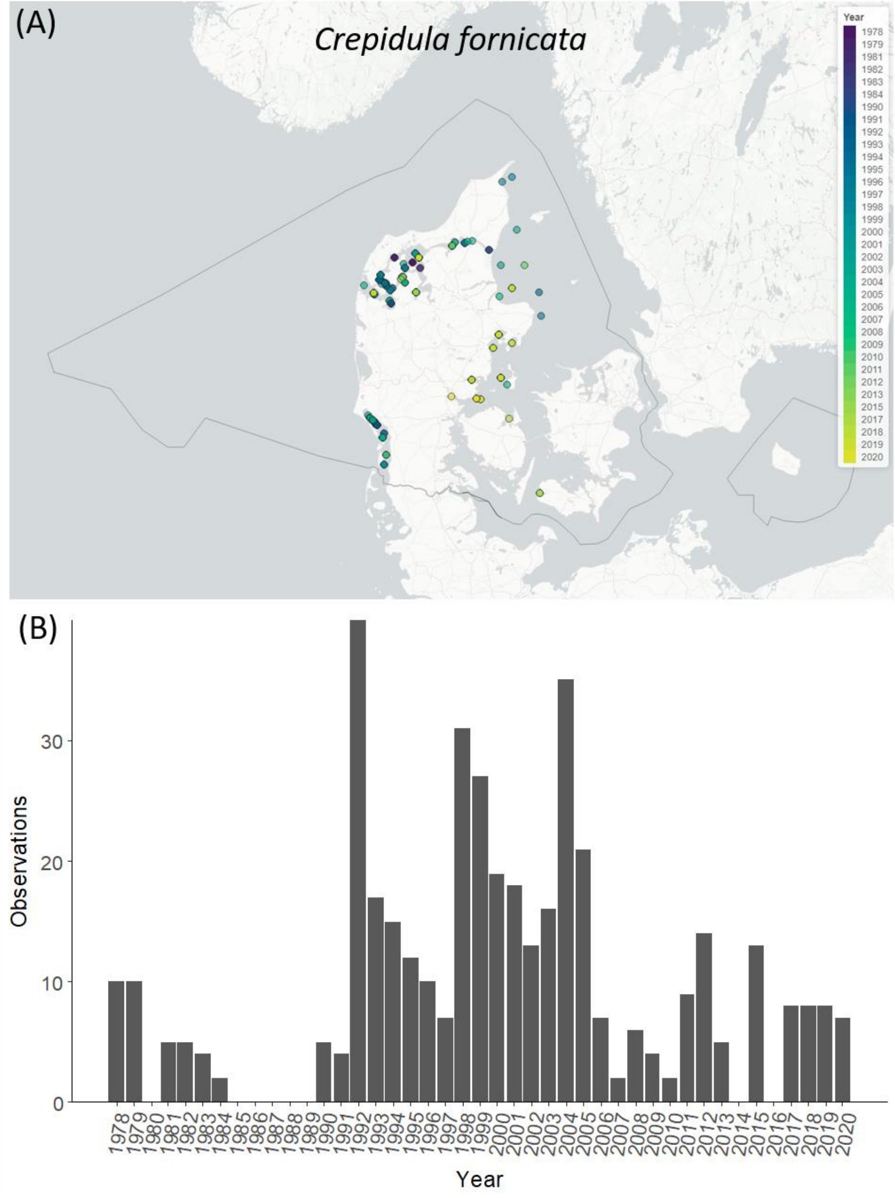

Figure 13. Map showing distribution of *Crepidula fornicata* from the NOVANA database from the beginning of the monitoring project (**A**); occurrence in different years from all NOVANA stations (**B**).

Crepidula fornicata is highly tolerant to different environmental factors. It can tolerate slightly sub-zero temperatures for short periods, but winter mortality in cold winters with average temperatures below 2 °C was high [121]. On the other hand, it can also tolerate temperatures above 30 °C for short periods [122], but has optimum feeding and growth rates around 15 °C [123]. The planktonic larvae are more susceptible to temperature than the adults [124]. Salinity tolerance is somewhat restricted; 18–40 psu has been recorded from its native range [125]. Slipper limpets also seem to be tolerant of ocean acidification related to global warming [122]. *Crepidula fornicata* has significant tolerance to desiccation, which is most important for intertidal populations. Slipper limpets have high fecundity; one female can produce in excess of 60,000 eggs, which are deposited in capsules, each containing about 300 eggs. The female broods the eggs until planktotrophic veligers are released. Each female may spawn 2–4 times per year, and the spawning season extends through most of the year, except during the coldest months [126,127]. Larvae are planktonic for 7 to 27 days, depending on temperature.

When *C. fornicata* was first introduced to Europe, it was called "oyster pest" because it was assumed that it was a serious competitor for space and food. Many experimental studies have been published. A positive impact is that it may prevent harmful algal blooms by feeding on these species. It may also avoid predation on mussels by sea stars. However, mussels must spend extra energy producing more byssus when they have attached slipper limpets. *Crepidula fornicata* may occur in extremely high densities (up to 18 kg/m^2 has been recorded in oyster culture sites in France). The production of feces and pseudo-feces at such densities may significantly alter ecosystem functioning [117]. However, such high densities have not been reported from Danish waters.

Hemigrapsus sanguineus (De Haan, 1835) and ***Hemigrapsus takanoi*** Asakura and Watanabe, 2005. Asian shore crab and brush-clawed shore crab. The two small (1–3 cm) marine crab species are native to the coasts of the northwest Pacific regions. They are very similar, but they can be distinguished by the tuft of yellow bristles between the claws of the *H. takanoi* males (Figure 14) [128]. Juveniles are difficult to distinguish, and it is unclear if all reported occurrences have actually been correctly identified. Hence, we treat them under the same heading.

Figure 14. Male *Hemigrapsus takanoi*. Specimen from Dybsø Fjord, July 2018. Photo: M. and S. Mikkelsen.

The two crab species have a high tolerance to temperature fluctuations and can inhabit environments with salinity varying from 7 to 35 psu. However, completion of the larval development apparently requires salinities above 20 psu [129]. The fecundity of the two species is high: 40,000–50,000 eggs in one brood of a large female. The females brood eggs and embryonic development times depend strongly on temperature [130]. The planktonic larval phase is about one month, depending on temperature and salinity [131], which promotes the dispersion of the species. The species appear to be very opportunistic in habitat choice, but prefer habitats along the coastline and artificial structures, such as harbors. In Denmark, the two species have successfully inhabited a biogenic reef constructed by another alien species, the Pacific oyster, *Magellana gigas* [128].

Many unanswered questions still remain about the invasive effects on the ecosystems in Denmark caused by the invasion of the two *Hemigrapsus* species. The crabs eat smaller mussels, which might affect the mussel stocks. There are few common native crab species along the coastline, but the native European shore crab, *Carcinus maenas* (in other parts of the world seen as an invasive species), could be a competitor to the *Hemigrapsus* species for habitat and food. All three species seem to prefer animal prey (they all predate on mussels) rather than algae. Studies from the German part of the Wadden Sea show that adult *Hemigrapsus* spp. predate on small, juvenile *Carcinus maenas,* whereas the opposite does not seem to be the case [132–134].

In Europe, *H. takanoi* was registered first in La Rochelle, France, in 1994 and *H. sanguineus* in Le Havre, France and Oosterschelde, The Netherlands, in 1999. The species probably spread from Asia by ship ballast water and were introduced to the North Sea coast, where a secondary spread took place northwards. The first time the two species were found in Danish waters was on the Danish island Rømø in the Wadden Sea in 2011 [135].

The species are not easily registered in the Danish monitoring program (only one observation from the Wadden Sea area of *Hemigrapsus takanoi* in 2015), so most of the observations have been obtained through citizen science. The species are difficult to distinguish and are described together in terms of spreading.

Data from Arter.dk (a national database supported by the Ministry of the Environment) shows 66 observations of the species in the period 2011–2022 (Figure 15).

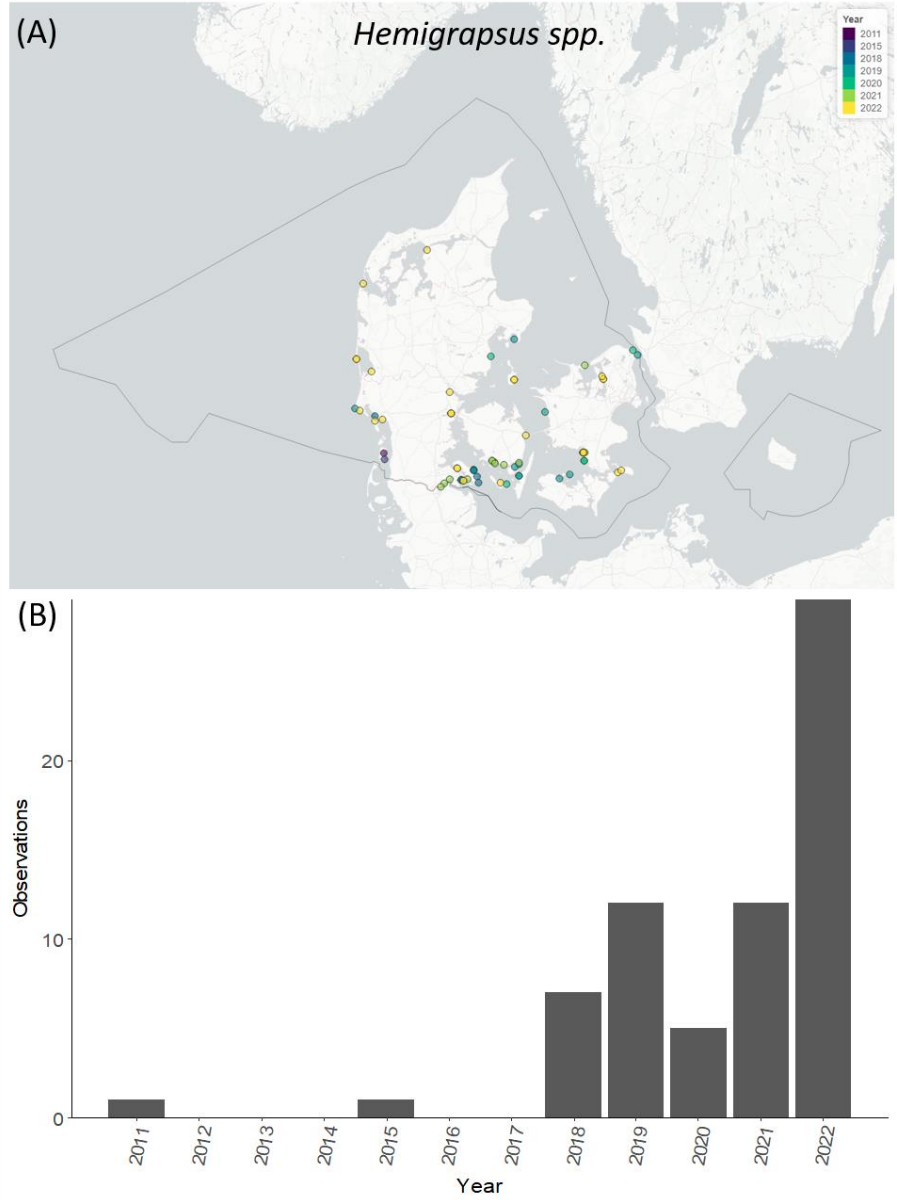

Figure 15. Distribution of *Hemigrapsus sanguineus* and *H. takanoi* 2011–2022 (**A**); occurrences of *Hemigrapsus* spp. during the same time interval (**B**). Data from Arter.dk and from ICES WGITMO annual national reports for Denmark.

From 2011 to 2018, they were known only from the Wadden Sea (records reported in ICES WGITMO reports from 2013, 2015, 2016). Arter.dk was not fully implemented with a user-friendly app until 2021, so many earlier records are from personal communications from fishermen, mostly shrimp fishers, who caught the crabs in their traps and sent pictures and specimens directly to the Natural History Museum of Denmark or to regional nature guides for identification. Most of these records have been published annually in national reports of the ICES Working Group of Introductions and Transfers of Marine Organisms, available from https://ices-library.figshare.com/WGITMO (accessed on 12 January 2023). Presently, *Hemigrapsus* spp. is present mostly in the Wadden Sea, the Belt Sea, and the western Baltic Sea, but they will most likely spread to other sub-regions over the coming decade.

In two areas, the Wadden Sea on oyster banks and the Dybsø Fjord, the species have established and can reach very high densities locally.

Sargassum muticum (Yendo) Fensholt, 1955 (wireweed). *Sargassum muticum* (Phaeophyceae, brown algae) is a perennial brown macroalgae native to the Northwestern Pacific (Japan). It spread to France via imported oyster spat in the 1960s, and from there spread to England (1970s), and was observed in the Netherlands (1980), Denmark, and Sweden (1984), and Germany and Norway (1988) [62,136].

Sargassum muticum grows attached to the hard substratum, smaller stones on the sandy bottom, or even as an epiphyte on other macroalgae at depths down to 6 m (Figure 16), but forms dense floating mats in late summer. Individuals of *S. muticum* can attain a size of 2–4 m [62].

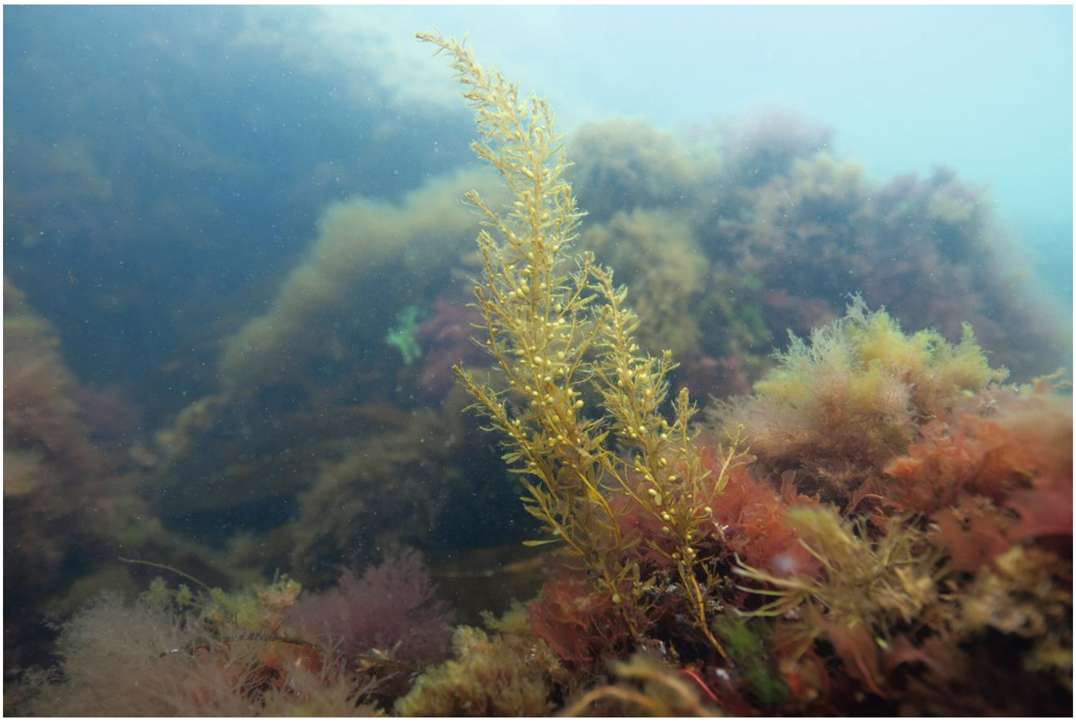

Figure 16. *Sargassum muticum* on boulder reef (Marselisborg Harbor) Photo: P. Bondo Christensen.

In Denmark, *Sargassum muticum* is established in areas with salinities above 16 psu and medium exposure. The species tolerates low light and a range in temperatures and expands in Denmark with an average speed of 7–8 km (up to 22.4 km) per year [137]. Expansion is limited by suitable hard substratum and reduced salinity toward the Baltic Sea.

Wireweed owes its high spreading potential to the ability to reproduce both sexually and vegetatively and spread via detached fragments with positive buoyancy thanks to the tiny characteristic air bladders that form part of the foliose tissue [62].

In Denmark, negative effects of *S. muticum* are expressed mainly as displacement of native perennial macroalgae and ecosystem engineers, such as the slower-growing *Halidrys siliquosa* and *Fucus* spp., which are inferior in the competition for light and substrate [138]. Where no significant direct effects on seagrass (*Zostera marina*) or species diversity in macroalgae communities have been documented, negative effects of free-drifting mats of *S. muticum* on the re-colonization of seagrass has been documented [139]. Furthermore, the faster and more complete decomposition *of S. muticum* as compared to native species increases the nutrient turnover and changes the biochemical cycles in areas with large populations of *S. muticum*, such as in the Limfjord [140].

For *S. muticum*, however, the documentation of positive effects on local biodiversity also exists, as the species generates increased macroalgae cover, serving as substrate for native marine invertebrates [137].

The large drifting mats of *S. muticum* can pose a nuisance to sailing, ship traffic, and fisheries. They can also, while decaying in late summer, contribute to oxygen depletion, produce an obnoxious smell, and reduce the recreational value in affected coastal areas. The species has no negative effects on human health and is a highly treasured food in Asia, albeit containing relatively high concentrations of arsenic [141]. In Denmark, critical concentrations of arsenic have not been documented, but still, the national food authorities recommend not consuming *S. muticum* often or in large quantities (https://www.foedevarestyrelsen.dk/Foedevarer/kend_kemien/Sider/Specifikke-foedevarer.aspx (accessed on 12 January 2023)).

Sargassum muticum has been registered in the Danish monitoring program since 1988, with 663 observations since and up to 2020, respectively (Figure 17).

Data from Arter.dk (national database supported by the Ministry of the Environment) shows 245 observations of *S. muticum* in the period 2011–2022, (not included in Figure 17 because they are not all confirmed by taxonomic specialists, and because some may be drift specimens stranded at the location of observation).

Gracilaria vermiculophylla (Ohmi) Papenfuss, 1967 (Worm Wart Weed, Black Wart Weed). *Gracilaria vermiculophylla* (Rhodophyta, red algae) is a perennial red macroalga native to the Northwestern Pacific (Japan) (Figure 18). The species was introduced to the east Pacific, the Mediterranean, and the east Atlantic via the fisheries and aquaculture industry and, potentially, also via ballast water. The species was first registered in Denmark in 2003 [61]. *Gracilaria vermiculophylla* initially grows attached to a hard substratum—smaller stones and shells—but form dense floating mats in late summer. Individuals of *G. vermiculophylla* grow up to 0.15–1 m in length [61].

As with *Pseudosolenia calcar-avis,* a discrepancy exists between the species name given by Algaebase and WoRMS. In WoRMS, *Agarophyton vermiculophyllum* is given as the accepted species name, and both *Gracilaria vermiculophylla* and *Gracilariopsis vermiculophyllum* are given as unaccepted synonyms. In contrast, Algaebase accepts *Agarophyton vermiculophyllum* as a synonym of *Gracilaria vermiculophylla,* and indicates *Gracilariopsis vermiculophylla* to be the basionym.

In Denmark, *Gracilaria vermiculophylla* is predominantly established in areas with salinities higher than 15 psu, but it tolerates salinities down to 10 psu. It has a preference for shallow, protected, nutrient-rich fjords with sandy or muddy sediments, where it grows attached to small stones and shells [142].

Gracilaria vermiculophylla has a high spreading potential due to its ability to reproduce both sexually and vegetatively and is capable of spreading via detached fragments [61].

Negative effects of *G. vermiculophylla* in Denmark are predominantly documented from the large floating mats either competing for light and nutrients or generating direct physical disturbance for the perennial native ecosystem engineers, macroalgae (*Fucus* sp.)

and seagrass (*Zostera marina*) [143–145], or from oxygen depletion stimulated by large decomposing mats of *G. vermiculophylla*.

As for *Sargassum muticum*, documentation of positive effects on local biodiversity exists, as *G. vermiculophylla* also generates increased macroalgae cover, serving as substrate for native marine invertebrates [144].

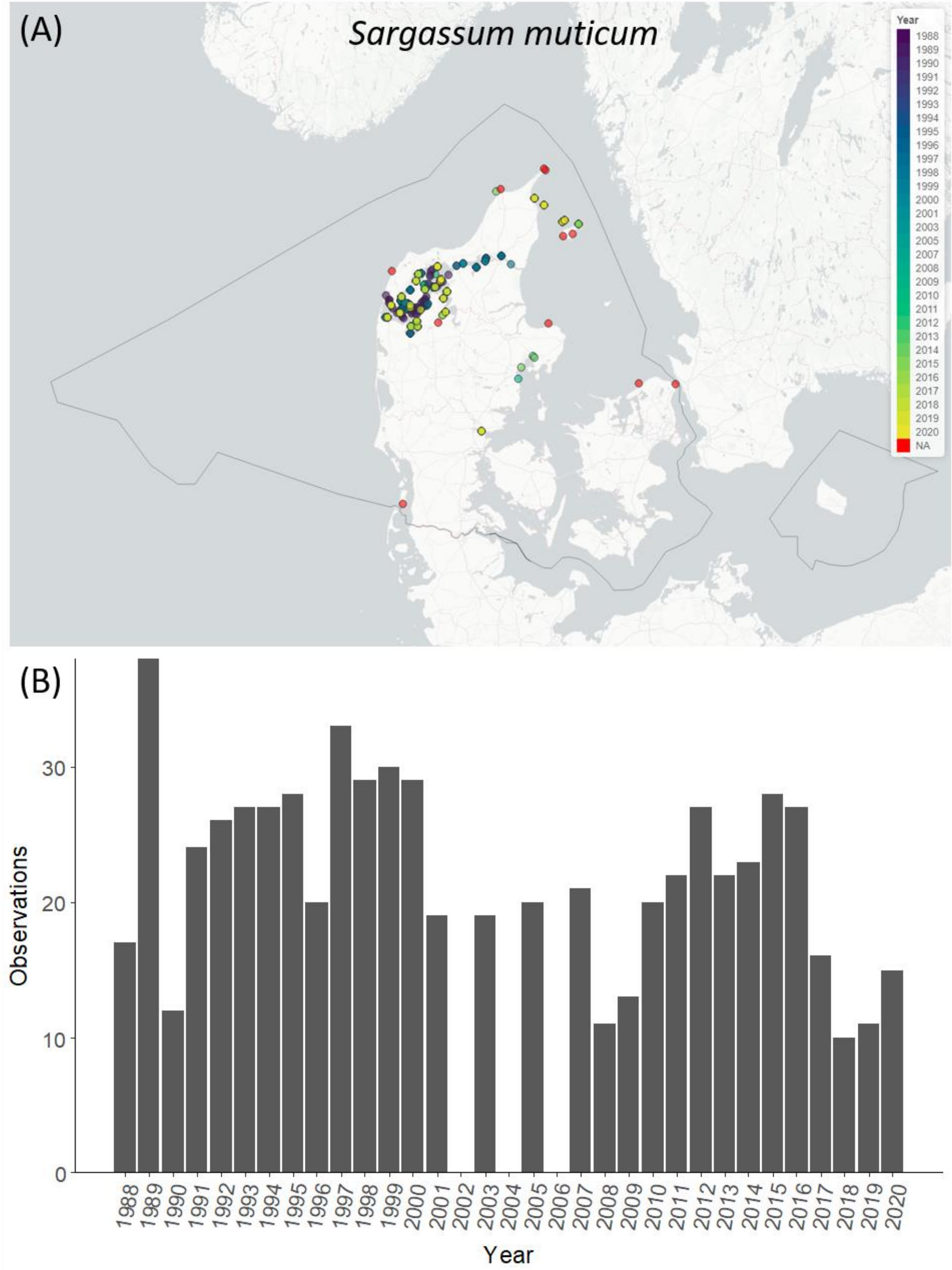

Figure 17. Distribution of *Sargassum muticum* in Danish waters (**A**); number of observations during the years 1988–2020 from the NOVANA database and from Nielsen et al. [62] (**B**). The red dots in (**A**) are records that are not included in (**B**).

Gracilaria vermiculophylla has no negative effects on human health. The species is cultivated and harvested commercially for food in other European countries [146].

Gracilaria vermiculophylla has been registered in the Danish Monitoring Program since 2007, with 164 observations between 2007 and 2020 (Figure 19).

Figure 18. *Gracilaria vermiculophylla* sampled from Begtrup Vig, Denmark (20th of September 2020). Photo by Karen-Lise Krabbe.

Data from Arter.dk includes 67 observations of *G. vermiculophylla* in 2011–2022 (not included in Figure 19 as distinguishing *G. vermiculophylla* from native *Gracilaria* species requires taxonomic experts [61]).

Neogobius melanostomus (Pallas, 1814), round goby. The round goby is native to the Ponto-Caspian region (Caspian Sea, Black Sea, Sea of Azov, Marmara Sea, and adjacent river systems). From here—especially from the Black Sea—the species has spread to other areas via artificial channels connecting river systems and via ballast water, and it is now one of the most widespread invasive fish species in both Europe and North America [147,148]. In the Baltic Sea, the round goby was first encountered in the 1990s and was quick to establish reproducing populations [149].

Since the first record in Danish waters—at the coast of Bornholm in 2008—the National Fish Atlas Project has closely monitored the distribution. In 2009, the round goby was caught near Bornholm once more, and it was also found in Guldborgsund between the islands of Falster and Lolland. In the following years, distribution increased at an alarming rate, and from 2008 to 2013, the expansion rate was estimated to be around 30 km/year [150]. In 2022, the distribution covered coastal areas in most of the southeastern part of Denmark around Bornholm, Møn, Lolland, Falster, Langeland, and Ærø, and also the southern and eastern parts of Zealand and Funen. It was even found in Randers Fjord at the northeast coast of Jutland (see Figure 20). In most areas, it also occurs in the adjacent freshwater streams. Even though the expansion rate has slowed down a little since the early observations, it is expected that the distribution will cover most of the Danish coastal areas in only a few decades. In many of the infected areas, the round goby has become one of the most common fish species. In Guldborgsund, the population was, as early as in 2012, estimated to be around 200 tonnes (fresh weight) [151].

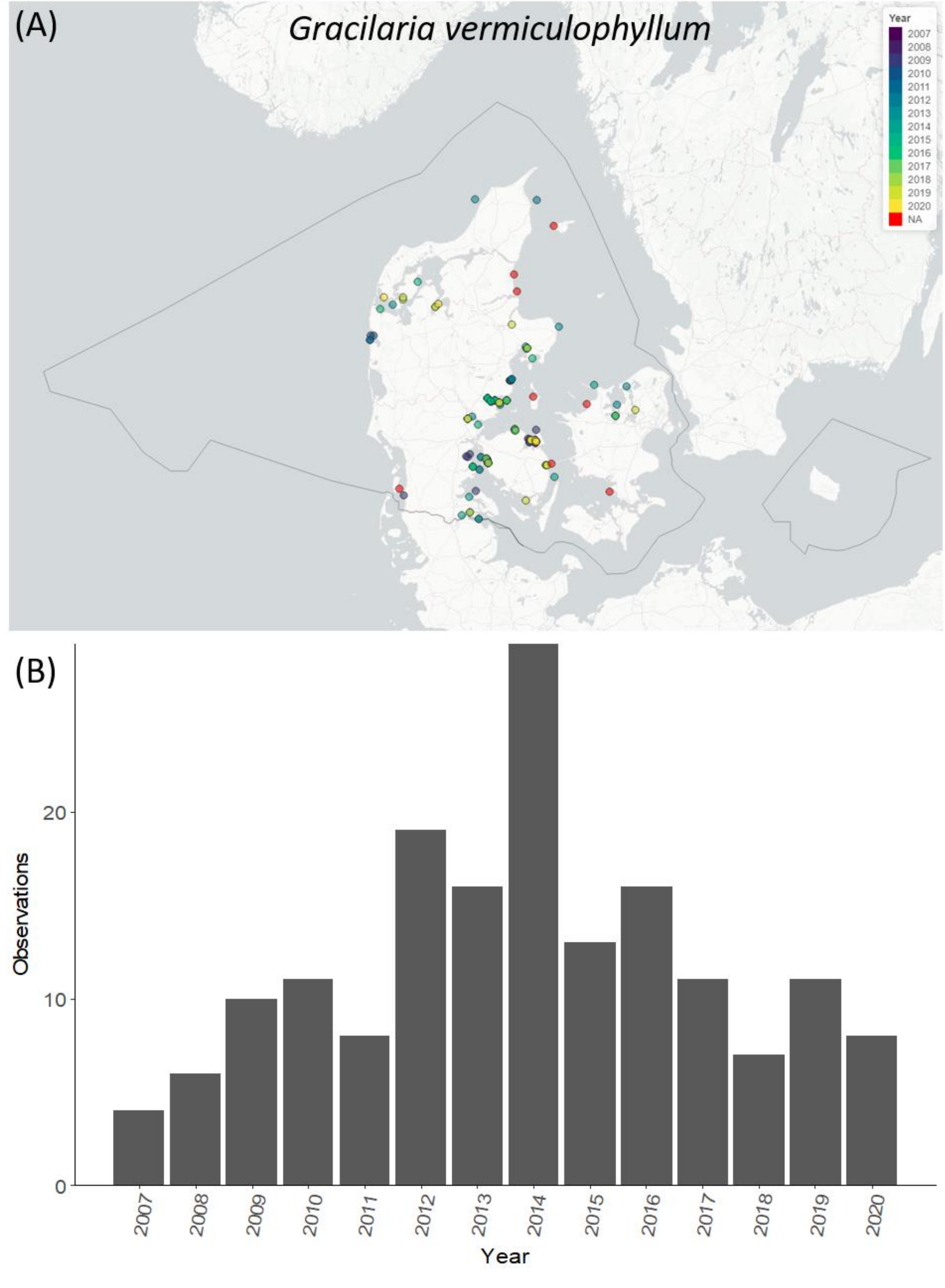

Figure 19. Distribution of *Gracilaria vermiculophylla* in Danish waters from 2007 to 2020 (**A**); number of observations during the years 2007–2020 from the NOVANA database and from Nielsen et al. [61] (**B**). For red dots in (**A**), see legend to Figure 17.

The round goby is a large species, and with a body length of up to 25 cm, it is much larger than any of the 13 native goby species from Danish waters (Figure 21). It is a coastal species rarely found deeper than 20 m and often most numerous from 1 to 5 m. It has a broad temperature range from around −1 to 30 °C [152], and it is a euryhaline species tolerating both freshwater and saltwater up to at least 30 psu [153]. Often the highest population densities are found in brackish water, and, in the vast brackish areas around Denmark, it has found a suitable habitat. Round gobies normally mature after 2–4 years, and breeding season is from April to September at water temperatures between 9 and 26 °C [154]. Females can produce up to around 5000 eggs per season. The eggs are attached to, for example, the underside of rocks and are guarded aggressively by the males until they hatch. Maximum age is at least seven years [150].

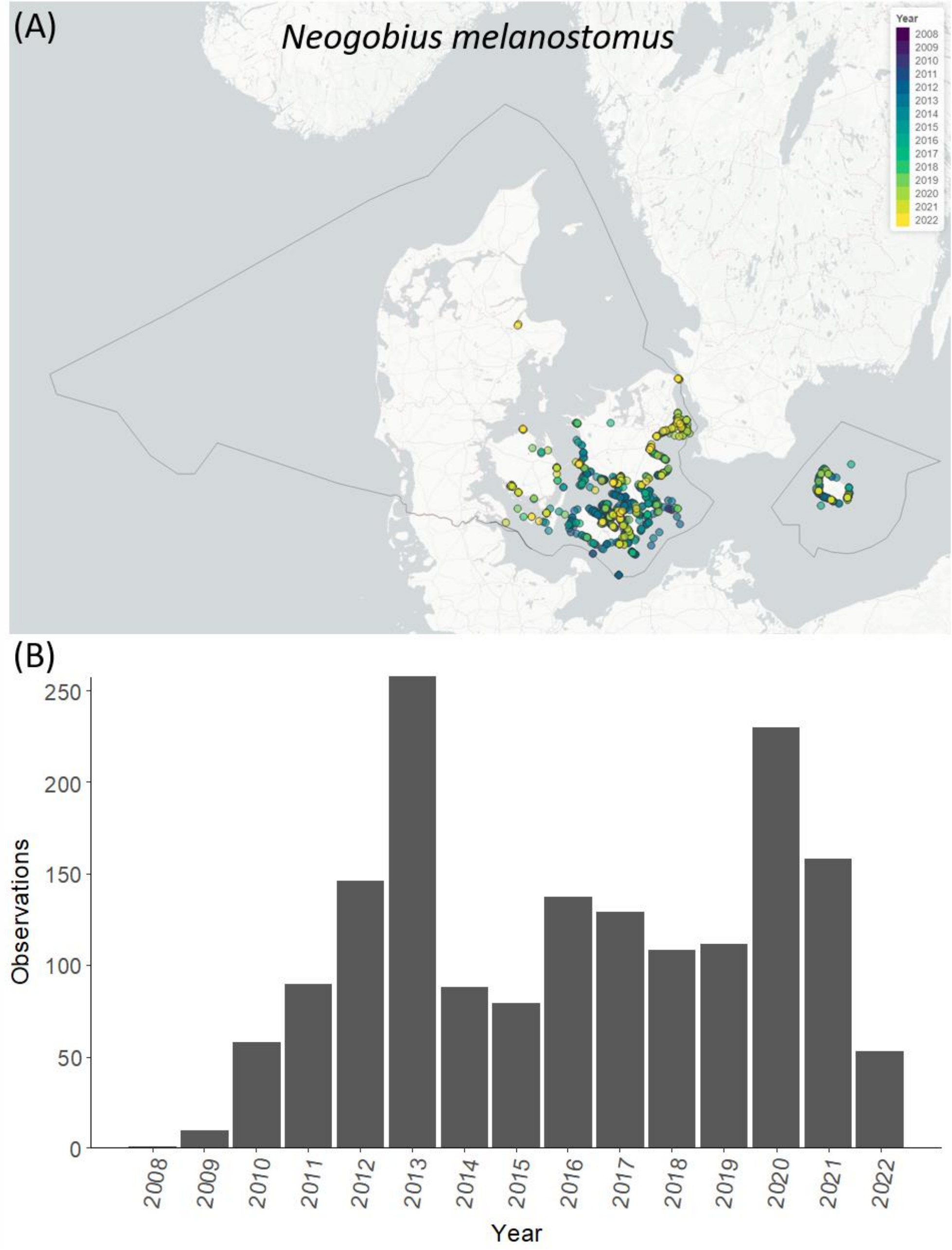

Figure 20. Distribution of *Neogobius melanostomus* from 2008 to 2022 (**A**); number of observations during the years 2008–2022 from the National Fish Atlas (**B**).

Due to the relatively recent invasion, the effect on other species and the environment is still uncertain. There is a direct competition for space and shelter with, for example, the native black goby (*Gobius niger*), which seems to lose the competition with the larger species and are reduced in numbers in the most heavily invaded areas. Local fishermen have primarily been worried about predation on Baltic shrimp (*Palaemon adspersus*), which is a species of relatively large economic importance in many brackish areas. Still, studies have shown that small snails and bivalves are the primary food. Negative changes in length–weight relations in round gobies from Guldborgsund, imply that the gobies started to starve after having grazed down the small invertebrates after only a few years [150]. Another study has confirmed changes in the invertebrate community—tiny bivalves and snails [155]. Among other negative impacts, a resuspension of sediment can be problematic, as round gobies dig holes in search of prey and shelter, and thereby may dislodge plants. There might, however, be a positive effect on predators, such as perch (*Perca fluviatilis*) and pike (*Esox lucius*), as the round goby shifts large biomass from small invertebrates to fish, which is a more suitable prey. In the Bay of Gdansk in the Polish part of the Baltic Sea, Bzoma and Stempniewicz [156] found that round goby accounted for 60% of the feed for the great cormorant (*Phalacrocorax carbo*) and other studies from the Baltic have found it to be feed for grey seal (*Halichoerus grypus*).

Figure 21. *Neogobius melanostomus*. Specimen from around Rødvig, May 2020. Length approx. 20 cm. Photo: H. Carl.

4. Discussion

4.1. Maintaining an Updated NIS List

Maintaining an updated list of NIS occurring in Danish marine waters is a dynamic, continuous process, which requires attention to taxonomic uncertainties, the documentation of new species, the gathering of information on the site of observation, and the incorporation of new taxonomic information. These challenges with updating and maintaining regional lists of marine NIS are not unique to the Danish seas, but a general concern for all European waters [17]. Comprehensive baseline reviews, such as [157], with information on introduction, pathways, donor regions, etc., for each species are rare, but highly valuable. National or regional checklists with or without annotations exist for most countries surrounding the North Sea and Baltic Sea (e.g., [158–161]. For Danish waters, benthic invertebrates and macroalgae have been reviewed in [28,29], which formed the historical baseline for the present study.

Data on new NIS arrivals in Danish waters has been gathered from a multitude of different sources. A significant source is the National Monitoring Program, NOVANA, which is continuously modified to meet the requirements of various EU directives and regulations and international conventions. As an initial step, non-indigenous species recorded during routine monitoring operations must be noted and entered into the database [162]. Beginning in 2021, separate samples have been collected in selected harbors, including settling plates and water samples for eDNA analysis [163]. The first data are still in the process of being analyzed. At present, data from other sources are at least as important, as almost 50% are derived from different data sources.

Non-indigenous species usually are first found associated with artificial structures, such as harbors, marinas, windfarms, and mariculture facilities. Such habitats have not previously been included in the National Monitoring Program, though they have been shown to be important in neighboring sea areas [3,161,164]. Several technical reports have been published in preparation for monitoring NIS in Danish waters [41,54,165–167]. These reports have reviewed the NIS occurring in Danish waters and sampled selected harbors for NIS using conventional and eDNA methods. This resulted in identifying a few NIS that had not been collected in Danish waters previously. Another source of detection of NIS is Environmental Impact Assessment reports in connection with offshore activities or coastal reclamation projects. The amphipods *Caprella mutica* and *Grandidierella japonica* were found in this way [168,169]. Verifying species identity is necessary for both of these sources, and uncertainties have been mentioned for some of the species only found once [41].

Several NIS have first been discovered by citizens, such as sport divers, anglers, birdwatchers, yachters, etc., who spend time in, on, or by the sea. Mobile phone cameras have made verifying such random observations easier, though some species need verification by microscopic examination or DNA sequencing. Smartphones also make geo-referencing observations made by the public possible. Furthermore, citizen science programs are relatively cheap compared to standard monitoring programs or baseline surveys [170].

Besides gathering information on new sightings of NIS, it is also necessary to regularly check up on the status of species already on the list. New taxonomic revisions may change the name of a species and its status from NIS to cryptogenic or maybe even native. In the case of splitting species and describing new species that are only known from the type locality, it may not be possible to decide the status. This seems to be the case for the polychaete worm *Tharyx killariensis* (see p. 6. Sometimes it is necessary to check old synonyms to determine the first observation of a species. We have also found a case where a species had been misidentified in the scientific literature, and only re-examination of specimens by a specialist resulted in correct identification.

Large species, such as *Sargassum muticum*, *Magallana gigas*, and the Japanese oyster drill, *Ocinebrellus inornatus*, may be discovered very soon after their first introduction, but small species, such as *Mnemiopsis leidyi* and most polychaetes, bryozoans, amphipods, and planktonic lifeforms are only noticed when they have become abundant, at least at one locality. In some cases, evidence can be found that they have been present at least a few years before their first observation. This makes it difficult to determine the pathways and vectors for such species, and although secondary dispersal from neighboring countries may be suspected, this cannot be verified. In this context, molecular tools hold great promise to compare population structure between different invaded sites and also to compare invasive and native populations, which can further shed light on the invasion vector and propagule pressure [171].

4.2. Trends in New NIS Arrivals

The NOVANA database from the Danish National Monitoring Program contains long time series from repeated sampling at specific stations. Many NIS are included, especially in soft bottom substrates and/or associated with macroalgae or boulder reefs. However, some species are under-represented, and others are missing. This is particularly the case for all jellyfish, gelatinous macrozooplankton, ichtyoplankton, and large mobile species, such as crabs and shrimps, and also for epifauna species in shallow water, such as barnacles. In this connection, amphipods should probably be considered mobile because very few observations of non-indigenous amphipods are present in the NOVANA database. The

NOVANA project was established to detect trends in the environmental status of various ecosystems, with the main focus on eutrophication. Although several methodologies have been applied, the spatial coverage and time intervals between samples from the same station do not permit the detection of the sudden appearance of newly introduced species in any habitat. As outlined above, the lack of incorporating *M. leidyi* or other species into National Monitoring Programs hampers our understanding and the ability to document detailed food web interactions. This highlights the necessity for coordinated efforts and the inclusion of all trophic levels into National Monitoring Programs to understand and detect non-indigenous species early.

It is noticeable that about half of the NIS have unknown pathways. This is most likely because they are only noticed when they become abundant, at least in one locality. For a number of species several pathways are suspected, indicating more than one introduction event. Secondary spread and ballast water are the dominating pathways for species with known pathways. This points to the importance of adhering to the provisions of the Ballast Water Convention.

In this study, we have emphasized the difference among sub-regions within Danish waters, i.e., the status of the Limfjord as a hotspot for the arrival and establishment of new NIS. This may both be caused by the sheltered status and relatively high salinity, but also oyster fishery and culture have been a source of introduction and detection of NIS. In recent times, the monitoring for harmful algae performed by mussel aquaculturists has been a source for detecting new phytoplankton species. Furthermore, the first observation of the parasite *Bonamia ostreae* was performed during the routine veterinary control of oysters from the Limfjord [172]. Reporting for the Ballast Water Convention distinguishes between OSPAR and HELCOM regions, whereas reporting for the MSFD uses the separation of Baltic and Greater North Sea waters proposed by the European Environmental Agency (EEA).

Until around 1980, there was a steady increase in the annual rate of NIS introductions. After this period, the rate at which new NIS were observed increased and remained high. While the effect of the NIS monitoring effort has likely affected the rate of new NIS observations, the onset of the 1980s also marks a period with a tremendous increase in global trading, raising the likelihood of new NIS introductions via shipping [173], which is reflected in the importance of shipping as a pathway for NIS introductions in the NE Atlantic [174]. Several NIS species were, furthermore, deliberately introduced via aquaculture (e.g., Pacific oyster and associated flora and fauna) during the 1980s, and the introduction of NIS from neighboring seas (secondary spread) has likely also influenced the rate of new NIS arrivals [174]. On top of this, increasing seawater temperatures with climate change are likely to have facilitated the expansion of warmer adapted NIS species through secondary spread from southern Europe into the colder northern regions, such as Danish seas [175,176]. NIS is often introduced through many pathways, with the likely effect of climate change further facilitating spread via secondary introductions [177]. The extent to which monitoring efforts, long-distance shipping intensity, and climate change have affected the rate of NIS introductions requires further analysis. Similarly, efforts should be made to fill our knowledge gaps in the pathways of NIS introductions into the Danish seas. Such information on the importance of environmental changes, human pressures, and vectors of introduction is pivotal for implementing proper mitigating measures to reduce NIS arrivals and impacts on indigenous species and receiving habitats.

4.3. Expert Evaluations

Setting the criteria for what constitutes an invasive species is a complex task, and existing methodologies need to be modified as knowledge about potentials for dispersal and impacts of NIS increases. Application of the Precautionary Principle is paramount for selecting tolerable levels for when a NIS can be considered invasive. This may not be the same for different countries, even within the same regional or sub-regional sea. Habitats deemed to have high conservation value in one country may not be rated the same in other countries.

Several methods for assessing the invasiveness of non-indigenous species exist, e.g., AS-ISK [178]. Most of them are rather complicated and require detailed information on the ecology and biology of individual species to assess whether their impacts are due to completion for food or space, high fertility, or broad tolerances of temperature and salinity, etc. The Harmonia procedure is fairly simple, but depends on the availability of appropriate expertise to evaluate species according to the six criteria. Economic and health criteria were included in our assessment exercise because this is a requirement of the EU Regulation on invasive species. However, they are not required by the MSFD and have not been used in the ranking of invasive species in the present study. The first evaluation of invasive species in Denmark was carried out in 2015 [179], and the present study's criteria have been slightly modified.

For a few of the NIS occurring in Danish waters, comprehensive risk assessments exist, either including Danish populations or from other European countries, e.g., *Magallana gigas* (formerly *Crassostrea gigas*) [63,180] and *Ensis leei* (formerly *E. directus* or *E. americanus*) [181], *Neogobius melanostomus* [68,155], and *Sargassum muticum* [137].

This study showed that the Harmonia protocol is appropriate for identifying which NIS can be considered invasive. However, it is less suitable for ranking species, except for the most invasive ones. After the top 3–5 species, many have identical scores and cannot be ranked. For the horizon-scan scoring, the problem is further complicated because some of the top-ranking species are rather unlikely to arrive in Danish waters in any foreseeable future. In contrast, species that can be considered "door-knockers" may score lower on invasiveness and impact, but are much more likely to arrive in the near future. In fact, a few of the species on this list have already been observed a few times, but have not yet established reproducing populations. For horizon scanning, the method outlined and tested in [182] has a better resolution for ranking species, but it is also more complicated. In the future, expert-based evaluations of invasiveness should be supplemented with quantitative assessment of impacts using available indicators, e.g., Olenin, et al. [183], or more recently proposed, knowledge-based impact categories, which, unfortunately, are only available for some of the most widespread NIS [184].

4.4. Temporal and Spatial Distribution of Selected NIS Species

The temporal and spatial dispersal of *Ensis leei* has been described in Knudsen [185] and Rasmussen [186]; that of *Rhithropanopeus harrisii* by Tendal et al. [187]; of *Magallana gigas* by Wrange et al. [188] and Hansen et al. [66]; and of *Mnemiopsis leidyi* by Tendal et al. [107], Riisgård et al. [112], and Jaspers et al. [36]. For *Sargassum muticum*, the invasion history was described by Stæhr et al. [137,138].

From the species selected here, a considerable amount of quantitative, geo-referenced information exists from many research projects on *Mnemiopsis leidyi*. For *Neogobius melanostomus* and *Sargassum muticum*, there is also good information on temporal and spatial distributions, but not many quantitative studies have been carried out in Danish waters. Although there are many observations of *Crepidula fornicata* in the NOVANA database, this species is most likely underrepresented because the habitats where it is often most abundant, i.e., shallow water mussel- and oyster beds, are not included in the National Monitoring Program. However, the high number of observations from the NOVANA program indicates that slipper limpets may be more common in deeper water than generally assumed. They also indicate that since 2011, the species has extended its range to southern Kattegat and the Belt Sea. This is very useful information. For the more recent arrivals, the *Hemigrapsus* species increase in distribution and the abundance of observations. This may also be a result of the increased availability of the citizen science website and database, Arter.dk. In 2022, several school classes made observations of these species in different locations.

It is difficult to make general conclusions on the distribution and abundance of NIS in Danish waters based solely on observations. However, combining observations with information on the environmental conditions governing the species presence and abundance is possible with species distribution models [189]. Such modeled probability maps of distribution and abundance will provide much needed information to improve the management of NIS and for the assessment of their impact. Different species show different patterns. Planktonic species may have spread throughout Danish waters in less than one year (e.g., *Mnemiopsis leidyi*). Benthic species with planktonic larvae may slowly move along the coasts, either of the North Sea towards Kattegat (e.g., *Ensis leei*), or from the Baltic Sea northwards through the Belt Sea (e.g., *Neogobius melanostomus* and *Rhithropanopeus harrisii*). The Limfjord is a hotspot for the arrival (or first observation) of NIS, and these species usually disperse from the west towards the east inside the fjord (e.g., *Sargassum muticum, Mnemiopsis leidyi*). The two *Hemigrapsus* species appear to be moving northwards in the North Sea and the Belt Sea.

Although the NOVANA program uses quantitative benthos samples, large species usually occur as singletons and calculations of biomass will not be scientifically meaningful. However, long-term studies in estuarine areas in the Netherlands have shown distinct lag-phases in biomass between first introduction, a "boom phase" a few years later, and a decline about a decade after first introduction [190]. Something similar has been observed for several NIS in Danish waters (see above for *Neogobius melanostomus*), although we do not have quantitative biomass data to support this.

5. Conclusions

In the present study, we have presented an ad hoc picture of information about marine non-indigenous species from Danish environmental authorities and other sources. We have included an updated list of 123 NIS (including cryptogenic species) as Supplementary Table S1. We have reviewed some of the problems associated with maintaining an updated list of all NIS occurring in Danish waters and presented some examples of problematic species. In the future, a more systematic collaboration should be established between authorities surveying harbors (including marinas), taxonomic expertise from natural history museums and universities, and citizen science projects collecting, verifying, and maintaining databases of casual observations of species.

At present, Arter.dk register species records with dates and locality. The latter can often be geo-referenced through GPS data from mobile phones. However, these records do not include information on whether specimens were empty shells, seaweeds washed up on the beach, or whether live specimens have been observed. This should be changed so that citizens can have their photos of shells or beached seaweed, but the database entry should have an annotation of the vital status of specimens recorded. Consulting companies performing EIA studies should be encouraged to register new observations of NIS (or presumed NIS) in this database with photos and voucher specimens, and the expert team of Arter.dk should assist in verification.

An increase in the rate of arrival (or detection) of NIS has been identified from 1980 onwards. This indicates that current management measures are insufficient or that secondary dispersal from neighboring countries is still the most important pathway of introduction in Danish waters.

The modified Harmonia protocol used in this study is suitable for identifying invasive species, but less suitable tor ranking invasive species. Other methods comprising more detailed impact categories should be applied as more information on specific impacts become available.

Developing indicators for temporal changes in the distribution and abundance of NIS seem challenging due to the species-specific patterns of dispersal, differences in habitat selection, and many other factors. Indicators for impacts could be developed as cumulative impacts of a number of the highest-ranking invasive species, as has been reviewed in [184]. An alternative to cumulative assessments is ecological network analysis (ENA) in the Wadden Sea, which demonstrated the trophic effect of invasive *Magallana gigas* and the Australasian barnacle *Austrominius modestus* [191]. Thus, using ENA on selected habitats where data is available could also provide insights into the response of the ecosystems affected by invasive species.

In a recent publication, Reise et al. [44] summarized both the negative and positive impacts of alien species in the Wadden Sea. Hansen et al. [66] also stressed some positive effects of biogenic reefs formed by Pacific oysters in the Wadden Sea and some in the Limfjord. Both these publications emphasized that maybe management measures towards invasive species should be restricted to habitats of special conservation value, e.g., Natura 2000 areas.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15030434/s1, Table S1: Current gross list (Excel file). Table S2: Extracts from NOVANA database of NIS species, from Arter.dk.

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