

Chapter 5

Spatio-temporal patterns of introduced seaweeds in European waters, a critical review.

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Abstract

Introductions of non-native species are a serious source of concern. A study on human-mediated transport of species demonstrated that rates of introductions have increased globally over the past centuries and averaged out over taxonomic groups there is no sign of saturation. Using seaweeds as a model group for the marine environment, a quantitative assessment of the temporal dynamics of primary and secondary introductions of seaweeds show that the rate of nonindigenous species being reported for the first time in European waters started declining since the beginning of the 1990's. To investigate whether this trend reflects a decline in the number of species being introduced or whether the discovery rate has declined because of factors other than the introduction rate, we analyzed trends in the literature of introduced seaweed species. Contrary to the rate of newly introduced species, the rate of the total number of records remained constant since 1990, with 115-120 records being recorded annually. The number of papers and authors increased spectacularly from 1970 to 2000 but shows a decrease from then onward. The combination of trends is interpreted as a decline in the rate new are yearly being introduced. Classifying introduced species according to geographical origin, the decline is mainly attributable to lower numbers of nonindigenous species with a NW Pacific origin being recorded from Europe, while the discovery rates of Lessepsian species or species native to Australasia has remained constant over the years. Given that livestock transfer of shellfish is the principal vector for the introduction of NW Pacific species, it appears that the increased awareness of authorities and stakeholders, and the implementation of policies dedicated to the prevention of introductions, reduce, but not prevent, the introduction of nonindigenous species.

Introduction

Over the last centuries thousands of species have dispersed outward from their native regions through human-mediated transport and have established populations in distant parts of the globe (Williams & Smith, 2007; Molnar et al., 2008). Many of these organisms have profoundly affected the abundance and diversity of native biota in the regions they have invaded (Vilà et al., 2010; Gallardo et al., 2016a), and in some cases they have had substantial economic impacts (Lovell et al., 2006; Holmes et al., 2009). A global analysis of temporal dynamics of species introductions by Seebens et al. (2017) demonstrated that the rate of introductions has significantly increased over the past centuries. Furthermore, over all taxonomic groups there are no signs of saturation and for most taxa the rate of introductions is still increasing. This trend has been linked to intensified global trade and transport (Seebens et al., 2013).

Because of differences in relative importance of the vectors for different groups of organisms in marine and terrestrial ecosystems, examining spatial and temporal patterns of specific taxonomic groups can inform policy makers about the effectiveness of targeted measures taken to mitigate the influx of nonindigenous species.

Here we present data on the patterns of marine species introductions and their spread at a European scale, using seaweeds as a model group for this assessment on marine environment. Representing one of the largest groups of marine aliens, constituting between 20 and 29% of all marine introduced species in Europe (Schaffelke et al., 2006), seaweeds are particularly fit for the purpose. Furthermore, they are attached and non-motile, reducing sampling errors caused by individual movement of target organisms. In addition, they comprise representatives of three major phyla, which, though widely divergent phylogenetically, have a series of convergent functional forms. In coastal systems, particularly on rocky shores, seaweeds are the dominant primary producers, playing a central structural and functional role in several habitats ranging from turfs to kelp forests (Mineur et al. 2015). Large-scale substitution of dominant native seaweeds with alien species may alter coastal productivity and food web structure, and therefore impact ecosystem services. Impact studies on invasive seaweeds have been carried out worldwide, and these have detected a range of ecological effects, mostly highlighting reduction in abundance of native biota (Williams & Smith, 2007). Maritime traffic and livestock transfer in aquaculture, in particular oyster cultivation, are usually regarded as the main vectors for primary introductions of alien seaweeds to Europe (Wallentinus, 2002; Mineur et al., 2012, 2015). A fragmented and to some extent incoherent policy

set up at EU and national levels, should prevent or limit introductions of marine organisms in European waters (Mineur et al. 2014). Directly relevant, although originally implemented only to mitigate the spread of diseases, are regulations of shellfish transfer within Europe and restrictions on the import of livestock from outside of Europe (Mineur et al., 2014). Although posing a reduced risk toward the introduction of nonindigenous seaweed species, similar measures have been taken to reduce the risk of introductions by hull fouling or ballast water discharge (Flagella et al., 2007; Mineur et al., 2008). Despite the environmental risk imposed by nonindigenous seaweeds, a comprehensive overview of the spatial and temporal dynamics of introductions in Europe is lacking. Overall scarcity of baseline data, which species have been introduced, the rates of introductions versus the rates of discovery and regional patterns of introduced species, fall short to test the effectiveness of prevention policies and therefore limit prevention of further introductions.

To address this knowledge-gap we compiled a database of nonindigenous seaweed species and distribution records in Europe, their likely origin and introduction vectors. These data are used to provide a quantitative assessment of the spatio-temporal dynamics of primary and secondary introductions in Europe. A comparison of discovery rates with statistics of the number of papers and the size of the phycological community that reports on nonindigenous seaweeds is used to infer conclusions on the introduction rates.

Materials and methods

Data compilation

We compiled a database of non-native marine seaweed species records reported from the Northeast Atlantic, Mediterranean and Macaronesian coasts (the Azores, Canary Islands, Cape Verdes, and Madeira). We report the year of the first report of the nonindigenous species in these three regions. Where possible this date refers to the year the species was first observed. In the absence of such information the date refers to the year the first record was published. If unclear when the species was introduced a question mark is added. The dataset, which includes published and unpublished records produced by various local and European research projects, builds on previous lists by Mineur et al. (2010) and Verlaque et al. (2015). Data from Macaronesia are based on Gil-Rodríguez et al. (2003) and Gallardo et al. (2016).

Refinements to previous lists were needed because in the past the term introduced species has likely been used too liberally. The introduced nature of certain species

was sometimes based on scanty evidence. In the present database we hope to remedy this by critically revising the list of nonindigenous seaweeds and by explicitly expressing confidence in the taxonomy and introduced nature of the species. First, species are considered nonindigenous when their presence in a given region is the result of a displacement linked to human activities either through a transport vector, or through the removal of a physical barrier, e.g. between the Red Sea and the Mediterranean Sea through the opening of the Suez Canal. The dataset also includes indigenous European species that have demonstrably become displaced within Europe as a result of human-mediated exchanges. Examples include exchanges of species between Atlantic and Mediterranean shores. However, true cosmopolitan species, whose current distribution may have been shaped by human transport, were omitted. Second, given widespread taxonomic uncertainty that surrounds many algal names we assigned an index of taxonomic accuracy for every species. We assigned a 'high' score to accepted nominal species that were not shown to be a species complex based on molecular studies in their European introduced or native ranges. A high score was also assigned to species for which, so far, there is sufficient confidence in unambiguous identification based on morphology. Conversely, species that belong to an understudied complex of cryptic species are assigned a low score. Related to, but not necessarily equivalent to taxonomic uncertainty, is the confidence that a species is indeed nonindigenous in European waters. To this end, we introduced a separate category, 'xenoticity'. In addition, we indicate the introduction status on an ordinal scale, ranging from not recorded, to recorded but not known to be established, likely established with recurrent observations or abundant in restricted areas, to widespread and abundant. If doubt exists regarding the introduced nature of a species in any of the three regions, this is indicated as 'potentially native'. Third, for each species an estimate is provided for their native biogeographical range. To do this, global distribution data were obtained from Algaebase (Guiry & Guiry, 2017). Indices of confidence of native ranges were assigned to each marine biogeographic region. Null values correspond to absence of records, medium indices to the presence of the species without a high confidence in stating if this biogeographic realm is the native range, while high indices are given to biogeographic regions that can be unambiguously determined as the origin, in the native range, of the populations present in Europe. We note that European populations may however have transited through other marine realms by secondary introductions.

Statistical analyses

Distribution data were gridded on raster cells of 100 km x 100 km (10,000 km²). The statistical analysis of spatio-temporal patterns was restricted to records until the year

2010, to avoid a potential bias due to lags in the reporting of nonindigenous seaweed species. We fitted three functions (linear, power and logistic) to the cumulative plots of the number of introduced species and the number of distribution records with the R package *minpack.lm*. The distribution of the AIC values and the midpoint of the logistic curve have been estimated from 1000 bootstrap samples. Additionally we fitted a local regression (LOESS) to these same cumulative plots and calculated the yearly rate of change in the number of introduced species and distribution. The span was calculated automatically by minimizing the AICc of the LOESS curve using the R package *fANCOVA*. Visualisation of hotspots of introductions is based on binned kernel density maps for the first record of every introduced species and for all distribution records with the R package *KernSmooth*.

Results

List introduced seaweeds: uncertainty in the numbers

In total 153 seaweed species have been listed as introduced in Europe, of which 104 species are red algae (Rhodophyta), 29 brown algal species (Phaeophyceae) and 20 belonging to the green lineage (Chlorophyta, Charophyta) (Fig. 1A; Table 1). However, an unequivocal link between specimens found in Europe with specimens in the native range has only been established for about half of these species. Given the widespread nature of cryptic and pseudocryptic diversity in algae in general it should come as no surprise that molecular studies have been substantially revising our view on many introduced species. For example, several species have been described from Europe which later turned out to represent introduced species. For example, *Dictyota cyanoloma* was described as a new species from the Mediterranean Sea and Macaronesia as recently as 2010 (Tronholm et al., 2010), but subsequent collecting efforts in Australia revealed that the species actually represent a cryptic introduction (Aragay et al., 2016; Steen et al., 2017). Similarly, *Porphyra olivii* described by Brodie et al. (2007) from the Mediterranean belongs to the same species as *Pyropia koreana* (Vergés et al., 2013). Obviously determining the nonindigenous nature of a species becomes much more difficult if introductions took place long ago as is the case for *Codium fragile* subsp. *fragile* and *Neosiphonia harveyi* which were established in Europe already by the mid-19th century as evidenced by herbarium records (McIlvor et al., 2001; Provan et al., 2008). A puzzling case is formed by several taxa with clear Indo-Pacific affinities which appeared in the Mediterranean Sea prior to the opening of the Suez Canal in 1869, *Acanthophora nayadiformis*, *Asparagopsis taxiformis* and *Ganonema farinosum*. At least for *A. taxiformis*, such a counterintuitive temporal pattern can be explained by the presence of two cryptic lineages, which include a

native strain present in the Mediterranean Sea prior to the opening of the Suez canal and a more recent introduction of an invasive strain (Chualáin et al., 2004; Andreakis et al., 2007). Such cases highlight the difficulty in establishing whether a species is introduced in Europe. Overall, only for about half of the species (54%) listed in Table 1, there is strong evidence that they are nonindigenous in Europe. For the remaining half the evidence is mediocre (35%) to weak (11%) at least. It should be noted that taxonomic uncertainty does not per se correlate with xenotocity. For several species there is good evidence that they are indeed nonindigenous, however, the taxonomy of the group is still not sufficiently established to be certain regarding the correct name of the species. Taxonomic uncertainty is not necessarily restricted to diminutive species which have been observed sporadically. *Agardhiella subulata* is a good example, its nonindigenous nature is not questioned, however, according to some authors the species should be identified as *Sarcodiotheca gaudichaudii* (Montagne) P.W.Gabrielson (Stegenga & Karremans, 2015). Likewise the correct taxonomic status of many of the introduced *Caulerpa* species found in the Eastern Mediterranean Sea (e.g. *C. lamourouxii*, *C. mexicana*, *C. scalpelliformis*) needs further study (Verlaque et al., 2000, 2015; Belton et al., 2014).

Taxonomic uncertainty and uncertainty regarding the introduced nature of seaweed species is most prevalent in the Macaronesian region. Out of 57 species present in Macaronesia no less than 27 have been given a low taxonomic accuracy score. Although several factors likely contribute to this uncertainty, the geographical location of the region, bordering the tropical Atlantic, contributes significantly to the difficulty in interpretation of the nonindigenous nature of species. Many tropical and subtropical taxa are reported from all major ocean basins. Very often these taxa represent (pseudo-)cryptic species complexes with the individual species being either range-restricted or widespread themselves. The lack of accurate baseline data regarding species boundaries and distributions makes it particularly hard to distinguish native from introduced seaweeds. Examples include *Caulerpa* spp., *Hypnea* spp., *Galaxaura rugosa*, *Ganonema farinosum*.

Table 1. Overview of the nonindigenous seaweeds in Europe, with indication of their presence in the NE Atlantic, Mediterranean Sea and Macaronesia (numbers = year of the first record, NA = not recorded, NT = Native, ? = uncertain | color codes: green = recorded but not known to be established, orange = likely established, recurrent observation to abundant in restricted areas, red = widespread and abundant, invasive, blue = (potentially) native). Taxonomic uncertainty is indicated in white = low, green = high. Xenotocity expresses the certainty that the species is indeed introduced (white = low, pale green = medium, dark green = high). Displacement (R = from remote geographical area; L = Erythrean migrant; M = NE Atlantic to Mediterranean, A = range extension in the NE Atlantic; U = unknown or ambiguous). Origin denotes the most likely native area (white = unlikely, pale green = potential, dark green = high likelihood).

Taxonomic name	Nr of Records	Region			Uncertainty			Origin					
		NE Atlantic	Mediterranean	Macaronesia	Taxonomic unc.	Xenotocity	Displacement	NW Pacific	Lessepsian	Australasia	W Atlantic	NE Atlantic	Indo-Pacific
Phaeophyta	1762												
<i>Acrothrix gracilis</i>	1	NT	1998	NA	0	0	R	1	1	0	1	1	0
<i>Ascophyllum nodosum</i>	2	NT	2009	NA	1	2	R	0	0	0	0	2	0
<i>Botrytella parva</i>	2	NA	1996	NA	0	0	R	1	0	0	0	1	0
<i>Chorda filum</i>	3	NT	1981	NA	1	2	M	0	0	0	0	2	0
<i>Cladosiphon zosterae</i>	1	NT	1998	NT	1	1	M	0	0	0	0	1	0
<i>Colpomenia peregrine</i>	172	1905	1918	1965	1	2	R	2	0	0	0	0	0
<i>Corynophlaea verruculiformis</i>	6	1994	NA	NA	0	1	R	2	0	0	0	0	0
<i>Corynophlaea cystophorae</i>	0	NA	NA	1993	0	1	R	2	0	0	0	0	0
<i>Desmarestia viridis</i>	6	NT	1947	NA	1	1	U	1	0	0	0	1	0
<i>Dictyota cyanoloma</i>	286	2008	1935	2007	1	2	R	0	0	2	0	0	0
<i>Ectocarpus siliculosus</i> var. <i>hiemalis</i>	1	NA	1998	NA	0	1	M	0	0	0	0	2	0
<i>Fucus evanescens</i>	33	1883	NA	NA	1	2	U	1	0	0	2	0	0
<i>Fucus serratus</i> [Iceland and Faroes]	58	1897	NA	NA	1	2	A	0	0	0	0	2	0
<i>Fucus spiralis</i>	1	NT	1987	NA	1	2	M	0	0	0	0	2	0
<i>Halothrix lumbricalis</i>	4	NT	1978	NA	0	1	U	1	0	0	0	1	0
<i>Leathesia marina</i>	3	NT	1905	NA	1	2	M	0	0	0	0	2	0
<i>Padina boergesenii</i>	20	NA	1965	NA	1	1	L	0	1	1	1	0	1
<i>Padina boryana</i>	1	NA	1993	NA	1	1	L	0	1	1	0	0	1
<i>Petalonia binghamiae</i>	20	NA	NA	1980	0	1	U	1	0	1	1	0	1
<i>Punctaria tenuissima</i>	6	NT	1957	NA	0	2	U	0	0	0	1	2	0
<i>Pylaiella littoralis</i>	1	NT	1960	NA	1	2	M	0	0	0	0	2	0
<i>Rugulopteryx okamurai</i>	1	NA	2002	NA	1	2	R	2	0	0	0	0	0
<i>Saccharina japonica</i>	2	NA	1976	NA	1	2	R	2	0	0	0	0	0
<i>Sargassum muticum</i>	924	1972	1981	NA	1	2	R	2	0	0	0	0	0
<i>Scytosiphon dotyi</i>	12	1987	1977	1993	0	1	R	1	0	0	1	0	0
<i>Spatoglossum variabile</i>	2	NA	1944	NA	0	1	L	0	2	0	0	0	1
<i>Sphaerotrichia firma</i>	1	NA	1970	NA	1	2	R	2	0	0	0	0	0
<i>Stypopodium schimperi</i>	22	NA	1973	1997	1	2	L	0	2	0	0	0	0
<i>Undaria pinnatifida</i>	171	1982	1971	NA	1	2	R	2	0	0	0	0	0
Chlorophyta	721												
<i>Caulerpa chemnitzia</i>	14	NA	1926	NT?	0	1	L	0	2	0	0	0	1
<i>Caulerpa cylindracea</i>	106	NA	1990	2002	1	2	R	0	0	2	0	0	0
<i>Caulerpa lamourouxii</i>	12	NA	1951	NA	1	2	L	0	2	0	0	0	1
<i>Caulerpa mexicana</i>	14	NA	1941	NT?	0	2	L	0	2	0	0	0	1
<i>Caulerpa scalpelliformis</i>	14	NA	1929	NA	0	2	L	0	2	0	0	0	1
<i>Caulerpa taxifolia</i>	87	NA	1984	NA	1	2	R	0	0	2	0	0	0
<i>Caulerpa taxifolia</i> var. <i>distichophylla</i>	17	NA	2006	NA	1	2	R	0	0	2	0	0	0
<i>Cladophora herpeticia</i>	10	NA	1948	NA	0	0	L	1	2	1	0	0	1

Taxonomic name	Nr of Records	Region			Uncertainty			Origin					
		NE Atlantic	Mediterranean	Macaronesia	Taxonomic unc.	Xenoticity	Displacement	NW Pacific	Lessepsian	Australasia	W Atlantic	NE Atlantic	Indo-Pacific
<i>Cladophora patentiramea</i>	1	NA	1991	NA	0	1	L	0	1	1	0	0	1
<i>Codium arabicum</i>	5	2003	2007	NA	1	2	L	1	2	0	0	0	1
<i>Codium fragile</i> subsp. <i>fragile</i>	397	1845	1950	1990	1	2	R	2	0	0	0	0	0
<i>Codium parvulum</i>	2	NA	2004	NA	1	2	L	0	2	0	0	0	1
<i>Codium taylorii</i>	23	2004	1955	?	0	1	R	0	1	0	1	0	1
<i>Derbesia boergesenii</i>	1	NA	1972	NA	0	1	L	0	2	0	0	0	1
<i>Derbesia rhizophora</i>	2	NA	1984	NA	0	2	R	2	0	0	0	0	0
<i>Halimeda incrassate</i>	3	NA	2011	2005	1	2	R	0	0	0	2	0	0
<i>Neomeris annulata</i>	1	NA	2003	NA	1	2	L	1	2	1	1	0	1
<i>Ulva pertusa</i> / <i>U. australis</i>	10	1993	1984	?	1	1	R	2	0	1	1	1	0
<i>Ulvaria obscura</i> (Kützinger)	2	NT	1985	NA	0	1	U	1	0	0	0	1	0
Charophyta	17												
<i>Chara connivens</i>	17	1979	NA	1975	0	1	A	0	0	0	0	0	0
Rhodophyta	2340												
<i>Acanthophora nayadiformis</i>	56	NA	1808	NA	1	1	L	0	2	0	0	0	1
<i>Acrochaetium balticum</i>	1	1998	NA	NA	0	0	A	0	0	0	0	2	0
<i>Acrochaetium robustum</i>	1	NA	1944	NA	0	0	L	0	2	1	0	0	0
<i>Acrochaetium spathoglossi</i>	3	NA	1944	NA	0	0	L	0	2	1	0	0	0
<i>Acrochaetium subseriatum</i>	3	NA	1944	NA	0	0	L	0	2	1	0	0	0
<i>Acrothamnion preissii</i>	62	NA	1969	NA	1	2	R	1	0	2	0	0	0
<i>Agardhiella subulata</i>	1	1973	1984	NA	0	1	R	1	0	0	1	0	0
<i>Aglaothamnion feldmanniae</i>	3	NT	1975	NA	0	1	M	0	0	0	0	1	0
<i>Aglaothamnion halliae</i>	24	1960	NA	NA	0	1	R	0	0	0	1	0	0
<i>Ahnfeltiopsis flabelliformis</i>	3	NA	1994	NA	0	2	R	2	0	0	0	0	0
<i>Anotrichium furcellatum</i>	39	1922	1939	1930	0	0	U	1	0	0	0	0	0
<i>Antithamnion amphigeneum</i>	38	1995	1989	NA	1	2	R	0	0	2	0	0	0
<i>Antithamnion densum</i>	21	1992	NA	1990	0	0	R?	1	0	0	1	1	0
<i>Antithamnion diminuatum</i>	2	NA	NA	1988	1	0	R	0	0	2	0	0	0
<i>Antithamnion nipponicum</i> / <i>A. hubbsii</i>	10	2003	1988	NA	0	1	R	2	0	1	0	0	0
<i>Antithamnionella boergesenii</i>	14	2004	1937	1921	1	1	R	0	0	0	2	1	0
<i>Antithamnionella elegans</i>	85	1961	1882	NA	0	1	R	2	0	0	0	0	0
<i>Antithamnionella spirographidis</i>	79	1927	1911	1974	0	0	R	2	0	0	0	0	0
<i>Antithamnionella sublittoralis</i>	5	NA	1980	NA	0	1	R	1	0	0	0	0	0
<i>Antithamnionella ternifolia</i>	113	1906	1926	NA	0	1	R	0	0	2	0	0	0
<i>Apoglossum gregarium</i>	11	NA	1992	NA	1	2	R	1	0	0	1	0	0
<i>Asparagopsis armata</i>	386	1923	1923	1965	1	2	R	0	0	2	0	0	0
<i>Asparagopsis taxiformis</i> [invasive strain]	39	2004	?	NT?	1	2	R	0	1	2	0	0	1
<i>Bonnemaisonia hamifera</i>	281	1893	1909	1930	1	2	R	2	0	0	0	0	0
<i>Botryocladia madagascariensis</i>	19	NA	1991	1988	0	2	R	0	0	0	0	0	1
<i>Caulacanthus okamurae</i>	23	1986	2004	NA	1	2	R	2	0	0	0	0	0
<i>Ceramium bisporum</i>	4	NA	2001	NA	0	1	R	0	0	0	2	0	0
<i>Ceramium strobiliforme</i>	15	NA	1991	1992	0	0	R	0	0	0	0	0	0
<i>Chondracanthus chamissoi</i>	1	2009	NA	NA	1	2	R	2	0	0	0	0	0
<i>Chondria curvilineata</i>	5	NA	1981	NA	0	1	R	0	0	0	2	0	1
<i>Chondria polyrhiza</i>	2	NA	1982	NA	0	0	R	0	0	0	2	0	1
<i>Chondria pygmaea</i>	14	NA	1974	NA	0	2	R	0	2	0	0	0	1
<i>Chondrus giganteus</i>	2	NA	1994	NA	1	2	R	2	0	0	0	0	0
<i>Chrysomenia wrightii</i>	15	2005	1978	NA	1	2	R	2	0	0	0	0	0
<i>Colaconema codicola</i>	7	1957	1952	NT	0	1	U	0	0	0	1	1	0
<i>Colaconema dasyae</i>	2	1983	NA	NA	1	1	R	0	0	0	0	0	0

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		NE Atlantic	Mediterranean	Macaronesia	Taxonomic unc.	Xenoticity	Displacement	NW Pacific	Lessepsian	Australasia	W Atlantic	NE Atlantic	Indo-Pacific
<i>Cryptonemia hibernica</i>	30	1971	NA	NA	1	1	R	0	0	0	0	1	0
<i>Dasya baillouviana</i>	21	1950	NT	NT	0	1	U	0	0	1	1	1	1
<i>Dasya sessilis</i>	43	1989	1984	NA	1	2	R	2	0	0	0	0	0
<i>Dasysiphonia japonica</i>	61	1994	1998	NA	1	2	R	2	0	0	0	0	0
<i>Devaleraea ramentacea</i>	1	1975	NA	NA	1	2	A	0	0	0	0	1	0
<i>Ezo epiyessoense</i>	1	1983	NA	NA	1	1	R	2	0	0	0	0	0
<i>Fredericqia deveauniensis</i>	4	1850	NA	NA	1	2	R	0	0	0	2	0	0
<i>Galaxaura rugosa</i>	3	NA	1990	NT	1	2	L	0	2	1	1	0	1
<i>Ganonema farinosum</i>	10	NA	1808	NT	0	0	L	0	2	1	1	0	1
<i>Gelidium vagum</i>	4	2010	NA	NA	1	2	R	2	0	0	0	0	0
<i>Goniotrichopsis sublittoralis</i>	11	1975	1989	NA	0	1	R	0	0	0	0	0	0
<i>Gracilaria arcuata</i>	9	NA	1931	NA	0	1	L	1	2	1	0	0	1
<i>Gracilaria disticha</i>	2	NA	1924	NA	0	2	L	0	2	0	0	0	1
<i>Gracilaria vermiculophylla</i>	80	1997	2008	NA	1	2	R	2	0	0	0	0	0
<i>Gracilariopsis chorda</i>	1	2010	NA	NA	1	2	R	2	0	0	0	0	0
<i>Grateloupia asiatica</i>	11	2010	1984	NA	1	2	R	2	0	0	0	0	0
<i>Grateloupia imbricate</i>	5	2014	NA	2006	1	2	R	2	0	0	0	0	0
<i>Grateloupia patens</i>	3	NA	1994	NA	1	2	R	2	0	0	0	0	0
<i>Grateloupia subpectinata</i>	20	1947	1990	1983	1	2	R	2	0	0	0	0	0
<i>Grateloupia turuturu</i>	85	1969	1982	1983	1	2	R	2	0	0	0	0	0
<i>Griffithsia corallinoides</i>	9	NT	1964	NA	0	1	U	1	0	0	0	2	0
<i>Gymnophycus hapsiphorus</i>	7	NA	NA	1989	0	1	R	0	0	1	0	0	0
<i>Herposiphonia parca</i>	2	2005	1991	NA	0	1	R	2	0	0	1	0	1
<i>Hypnea anastomosans</i>	2	NA	2008	NA	1	1	L	0	2	0	0	0	1
<i>Hypnea cornuta</i>	6	NA	1896	NA	1	2	?	1	2	0	0	0	1
<i>Hypnea flagelliformis</i>	1	NA	1956	?	0	2	U	1	2	0	0	0	1
<i>Hypnea flexicaulis</i>	3	NA	2009	NT	1	2	L	2	0	0	0	0	0
<i>Hypnea musciformis</i>	11	2003	NT	NT	0	0	U	0	1	1	1	0	1
<i>Hypnea spinella</i>	20	NA	1926	NT	0	1	?	1	1	1	1	0	1
<i>Hypnea valentiae</i>	3	NA	1996	NT	0	2	R	1	1	0	0	0	1
<i>Laurencia brongniartii</i>	1	1989	NA	NT	0	2	R	1	0	1	0	0	1
<i>Laurencia caduciramulosa</i>	11	NA	1991	NT	0	1	R	1	0	0	1	0	1
<i>Laurencia okamurae</i>	2	NA	1984	NA	1	2	R	2	0	0	0	0	0
<i>Lithophyllum yessoense</i>	1	NA	1994	NA	1	2	R	2	0	0	0	0	0
<i>Lomentaria hakodatensis</i>	26	1984	1978	NA	1	2	R	2	0	0	0	0	0
<i>Lophocladia lallemandii</i>	52	NA	1908	NA	1	2	L	1	2	1	0	0	1
<i>Mastocarpus stellatus</i> [Helgoland]	1	1983	NA	NT	1	1	A	0	0	0	0	2	0
<i>Monosporus indicus</i>	5	NA	2015	NA	0	1	L	0	2	0	0	0	0
<i>Neosiphonia harveyi</i>	109	1832	1958	1990	1	2	R	2	0	0	0	0	0
<i>Nitophyllum stellatocorticatum</i>	2	NA	1984	NA	1	2	R	2	0	0	0	0	0
<i>Pachymeniopsis gargiuli</i>	6	NA	2000	2007	1	2	R	2	0	0	0	0	0
<i>Pachymeniopsis lanceolata</i>	11	NA	1982	NA	1	2	R	2	0	0	0	0	0
<i>Palisada maris-rubri</i>	2	NA	1990	NA	0	0	L	0	2	0	0	0	1
<i>Pikea californica</i>	22	1967	NA	NA	1	2	R	0	0	0	0	0	0
<i>Plocamium secundatum</i>	4	NA	1976	NA	0	0	U	0	0	0	0	0	0
<i>Polyopes lancifolius</i>	2	2008	NA	NA	1	1	R	0	0	0	0	0	0
<i>Polysiphonia atlantica</i>	1	NT	1972	NT	1	1	M	1	0	1	1	2	0
<i>Polysiphonia morrowii</i>	23	1993	1997	NA	1	2	R	2	0	0	0	0	0
<i>Polysiphonia paniculata</i>	10	NA	1967	NA	0	1	R	0	0	0	0	0	0
<i>Polysiphonia schneideri</i>	2	2010	NA	NA	1	2	R	0	0	0	2	0	0
<i>Predaea huismanii</i>	1	NA	NA	1990	0	1	U	0	0	1	0	0	1
<i>Pterosiphonia pinnulata</i>	2	1990	NT	NA	0	2	U	1	0	0	0	0	0

Taxonomic name	Nr of Records	Region			Uncertainty			Origin					
		NE Atlantic	Mediterranean	Macaronesia	Taxonomic unc.	Xenoticty	Displacement	NW Pacific	Lessepsian	Australasia	W Atlantic	NE Atlantic	Indo-Pacific
<i>Pterosiphonia tanakae</i>	2	2005	1998	NA	1	2	R	2	0	0	0	0	0
<i>Pyropia koreana</i>	6	NA	2007	NA	1	2	R	2	0	0	0	0	0
<i>Pyropia suborbiculata</i>	12	2010	2010	1993	1	2	R	2	0	0	0	0	0
<i>Pyropia yezoensis</i>	2	1984	1976	NA	0	2	R	2	0	0	0	0	0
<i>Rhodophysemma georgei</i>	1	NT	1978	NA	0	1	M	1	0	0	0	2	0
<i>Rhodymenia erythraea</i>	1	NA	1948	NA	0	2	L	0	2	0	0	0	0
<i>Sarconema filiforme</i>	11	NA	1945	NA	0	2	L	0	2	1	0	0	1
<i>Sarconema scinaoides</i>	2	NA	1945	NA	0	2	R	0	2	1	0	0	1
<i>Scageliopsis patens</i>	12	2004	NA	1989	0	2	R	0	0	2	0	0	0
<i>Solieria dura</i>	3	NA	1944	NA	0	1	L	0	2	0	0	0	1
<i>Solieria filiformis</i>	4	1980	1988	2002	0	1	R	0	1	1	1	0	1
<i>Solieria</i> sp. [non described]	5	2005	2011	NA	0	2	R	1	0	1	1	0	0
<i>Spongoclonium caribaeum</i>	21	1973	1974	1980	0	1	U	1	1	1	1	0	1
<i>Symphyocladia marchantioides</i>	10	2004	1984	1971	0	1	R	1	0	1	0	0	0
<i>Vertebrata fucoides</i>	2	NT	1988	NT	1	1	M	0	0	0	1	2	0
<i>Womersleyella setacea</i>	92	NA	1986	1983	0	2	R	0	0	2	0	0	1

Records – temporal trends

A total of 4900 distribution records from published and non-published sources were compiled for this study. Nearly half of the distribution records (47%) concern the five most represented species: *Sargassum muticum* (925 records), *Codium fragile* subsp. *fragile* (397 records), *Asparagopsis armata* (386 records), *Bonnemaisonia hamifera* (279 records) and *Dictyota cyanoloma* (286 records) (Fig.1). These species have been the focus of dedicated research projects, are usually large in size, easy to identify on the field, and often have considerable population sizes. At the other end of the spectrum, there are 73 species with less than 5 distribution records of which 27 species have only been recorded once.

Breaking down the number of introduced species into the Mediterranean Sea, Atlantic shores and Macaronesia reveals that 63% of the introduced species have been reported for the first time in the Mediterranean Sea, 27% in the NE Atlantic and 10% in Macaronesia (Fig. 2A). Twelve introduced species are shared among the three regions, while one third of the species occurs nowadays in 2 regions (Fig. 2B). Most species are shared between the Mediterranean and the NE Atlantic (30 species), while a surprisingly low 5 species are shared between the Mediterranean and Macaronesia. The ratio of species belonging to red, green and brown lineages is approximately the same for the three regions but the Atlantic area has less introduced green and brown species than the Mediterranean area.

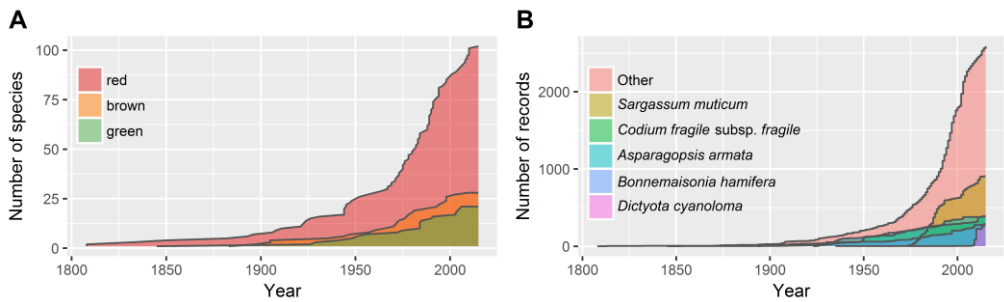


Figure 1. Number of introduced species and records through time in the whole study area. The left plot (A) shows the number of seaweeds introduced since 1800 for the red, brown and green classes. The right plot (B) shows the number of distribution records since 1800 of particularly well-studied introduced species in Europe: *Sargassum muticum* , *Codium fragile* subsp. *fragile* , *Asparagopsis armata* , *Bonnemaisonia hamifera* , *Dictyota cyanoloma* . In pink are the number of records for the remaining species. All curves are cumulative and superimposed.

A.

Region	Total	First	Red	Green	Brown
Mediterranean Sea	121	97	77	20	24
NE Atlantic	66	41	53	5	8
Macaronesia	31	15	21	4	6

B.

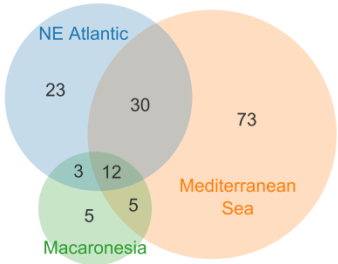


Figure 2. The left table (A) shows the total number of species reported in each European area; the number of species that has been reported for the first time in each European area, and the breakdown by red, green and brown algae of the total number of introduced species. The figure on the right (B) shows a Venn diagram of the number of the introduced species in the different areas.

The number of introduced species from 1950 to 2010, as represented by the date of the first record in Europe, was best fitted with a logistic curve (Fig. 3A). Likewise the total number of records of introduced species were also best presented by a logistic curve (Fig. 3B). For the bootstrapped AIC values of the different fitted curves we refer to Fig. S1 in Supporting information. The logistic curve implies that the number of new introduced species which are discovered is declining. Likewise, the accumulation rate of the number of distribution records of introduced species is also declining, albeit that the trend is less pronounced compared to the first record curve. These observations are confirmed by the rate of introduced species (Fig. 3C) which peaked in 1991, the sampling rate (Fig. 3D) which peaked in 1997 and by the midpoints of the logistic curves: 1986 for the number of introduced species and 1996 for the number of distribution records (Fig. S2 in Supporting information). The decrease in accumulation rate of nonindigenous seaweed species in Europe is at odds with general

trends as reported by Seebens et al. (2017) who observed a continuous rise in first record rates since 1800 for all groups of organisms except mammals and fishes.

Because the rate of discoveries of species are influenced by factors other than introductions (Costello & Sollow 2003), we also quantified the seaweed sampling effort along European coasts. We used the number of papers and number of unique authors reporting introduced seaweed species as a proxy for sampling effort (Fig. 4). These graphs disprove the idea that a decline in collecting or reporting effort underlies the slowdown in the number of first records.

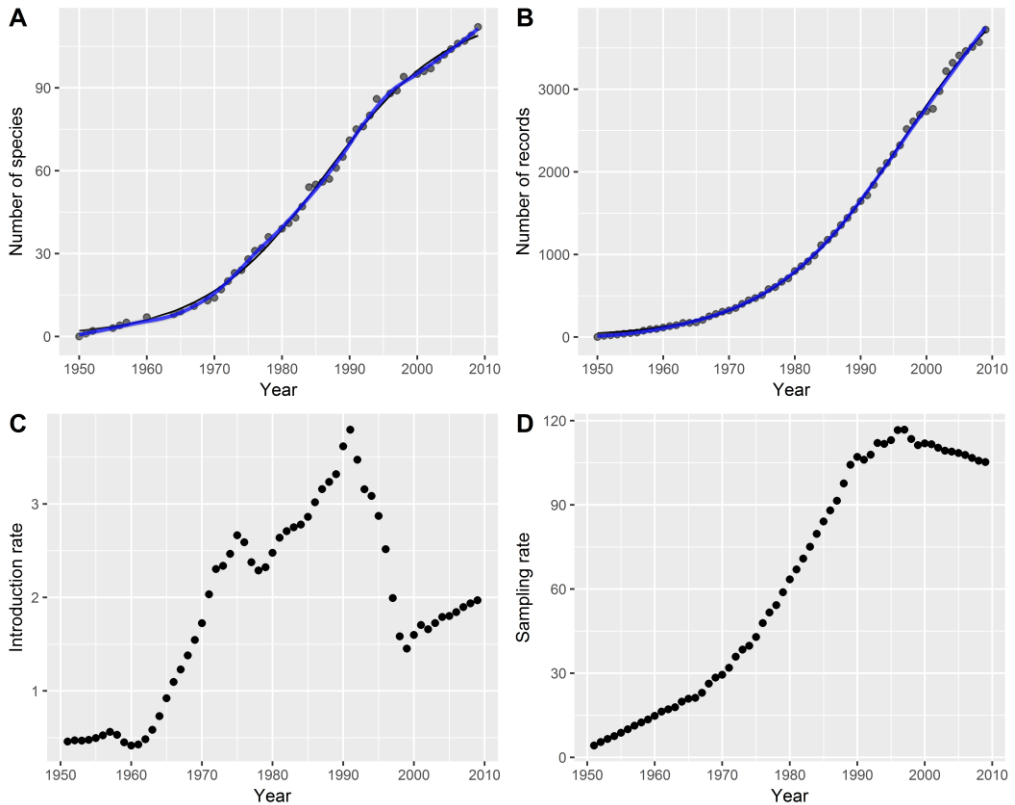


Figure 3. LOESS (blue) and logistic (black) curve fitting of the cumulative number of introduced species reported for the first time in Europe between 1950 and 2010 (A) and for the number of reported distribution records over all introduced species in the same area and period (B). The introduction rate (C) and the sampling rate (D) were calculated based on the fitted LOESS curves.



Figure 4. Number of unique authors per decade (A) and number of publications (B) reporting introduced species as a proxy for European sampling effort of introduced macroalgae.

The fact that such a decline in the introduction rate of non-indigenous species is apparently not shared with the majority of taxa or across geographic regions (Seebens et al. 2017), may reflect the somewhat atypical case of seaweed introductions and the success of measures aimed at mitigating new introductions. Contrary to most marine taxa, hull fouling and ballast water seem to play a relatively minor role only in the displacement of seaweeds across the globe. A disproportionate number of non-indigenous seaweed species appears to have been introduced through import of oyster stocks (Verlaque et al., 2007). In the late 1960s and early 1970s, disease outbreaks in Europe affecting oyster populations caused a major disruption of production. Mitigation procedures involved massive imports of oyster stock from the species' native range in the northwestern Pacific in the 1970s (Mineur et al., 2014). Alongside such stock imports non-native marine species were imported in great numbers from the northwestern Pacific to Europe. The accumulation curves of first records, which keep rising until the mid 1980s, mimic these imports. However it appears that European directives which authorizes all movements inside Europe and restrict shellfish stock imports from outside Europe reduce, but not prevent, the introduction of additional seaweed species.

Introduction hotspots

The importance of aquaculture toward introductions of seaweeds is reflected in the distributions of the first record of each species in Europe. A kernel density map (Fig. 5A) clearly shows the Thau lagoon, with 30 reports of first introductions in Europe (25%), as one of the major introduction hotspots in Europe. In total 58 species, 32% of the total seaweed diversity or 48-99% of the biomass, have been introduced in the Thau Lagoon (Boudouresque et al., 2010). The Thau lagoon is the epicentrum of oyster cultivation in the Mediterranean Sea. However, the oyster farmers rely entirely

on the import of juvenile oysters from other regions, European or non-European, because the lagoon is not suitable for oyster breeding. These continuous transfers result in astonishingly high numbers of introduced species. Upon closer examination, the Thau lagoon as well as other Mediterranean lagoons (Mar Piccolo, Venice lagoon), stand out with respect to introduction of native Atlantic species in the Mediterranean Sea (e.g. *Ascophyllum nodosum*, *Chorda filum*, *Cladosiphon zosterae*, *Pylaiella littoralis*, *Vertebrata fucooides*). A low native diversity due to the low occurrence of natural hard substrata in lagoons, and relatively recent construction of hard substrata for aquaculture purposes, concomitant with transfers of livestock which seed the new substrata, makes these habitats hotspots for nonindigenous species (Mineur et al. 2015). Most of these species actually fail to establish viable populations, and if persisting, their range in the Mediterranean Sea remains mostly restricted to the lagoon system. Differences in the abiotic physico-chemical environment between the Atlantic and Mediterranean likely underlie the failure of these species to spread widely in the Mediterranean. Nevertheless, repeated observations of Atlantic species in Mediterranean lagoons are evidence for continuous transfers of aquaculture livestock.

The Southeast Mediterranean accounts for 24 first reports, 58% between 1940 and 1960, and a total of 32 introduced species. The construction of the Suez canal in 1896 resulted in an open connection, between the northern Red Sea and the Eastern Mediterranean. As a result, 493 marine species are believed to have invaded the Mediterranean Sea through the Suez canal, so-called Lessepsian or Erythrean migrants (Zenetos et al., 2012). With respect to nonindigenous seaweeds many species were first reported in a series of papers by the Egyptian phycologist Anwar Aleem (1948, 1950). Recent efforts by Greek, Israeli and Turkish phycologists have expanded the list of Lessepsian seaweeds considerably and importantly have confirmed the identity of many species with molecular markers. Nevertheless, a paucity of baseline data makes it often difficult to establish the Lessepsian origin of many species or to point to the exact date of introduction. As outlined above reports of species with clear Indo-Pacific affinities which predate the opening of the Suez canal still puzzle phycologists. In addition the identity of many species reported for the first time by Aleem (e.g. *Gracilaria arcuata*, *G. disticha*, *Hypnea flagelliformis*, *Solieria dura*, *Spatoglossum variabile*) has never been confirmed using molecular markers and is highly uncertain. In general, the lack of solid baseline data hamper a detailed understanding of past and contemporary temporal dynamics of seaweed introductions in the Eastern Mediterranean Sea. More than in any other European region it remains difficult to link the observation of a new seaweed species with the

introduction date. This uncertainty bears down on the monitoring of migration through the Suez canal which is regarded as an ongoing process until present (Boudouresque, 1999). The current construction of the new Suez canal, doubling the capacity of the current corridor, is expected to increase the influx of Red Sea species (Galil et al., 2015) and contribute to the further tropicalization in the Mediterranean Sea (Bianchi, Carlo & Morri, 2003; Coll et al., 2010).

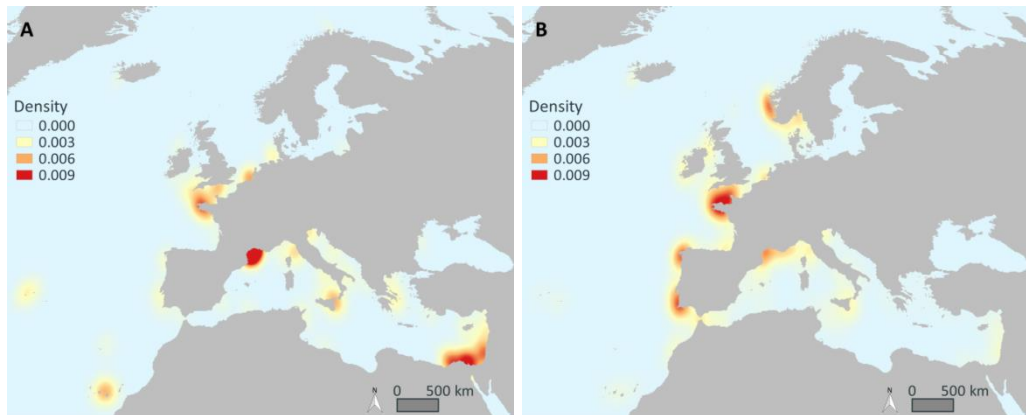


Figure 5. Binned kernel density maps of first introduction events (A) and of the distribution records of introduced species in our database.

Compared to the two Mediterranean hotspots, first reports appear less localized in the NE Atlantic. The Channel (Brittany, southern English coast) and the Scheldt estuary (the Netherlands) are most prominent as introduction hotspots. There is a high correlation between the introduction hotspots and the density map of all records of introduced species, indicative for high monitoring activities in areas where a lot of nonindigenous species are found (Fig. 5B). To some extent this spatial pattern may be influenced by the distribution of phycologists and research institutes. However, there is definitely not a one-on-one relationship between the density map of first reports and the map of all distribution records. Most strikingly, the Eastern Mediterranean Sea (Egypt, Israel) is a clear hotspot for first reports due to their proximity to the Suez Canal, but the total number of records from that region is rather low compared to Atlantic European coasts. On the opposite end of the spectrum, the southern Norwegian coast is particularly well-monitored even though no first records from that area have been reported.

Origin and spread

We mapped the distribution records of introduced seaweed species according to their presumed geographic origin or native range. Distribution records were gridded on a

100 x 100 km raster. Maps depict the number of species per grid cell for species of Northwest Pacific origin (Fig. 6A), Lessepsian migrants (Fig. 6B), Australasian origin (Fig. 6C) and the Northeast and Western Atlantic origin (Fig. 6D). The NW Pacific origin of 45 species is well established (Table 1). An additional 31 species are possibly native to the NW Pacific but there is no strong evidence at present (e.g. molecular sequence data) which support such a claim. Restricting analyses to species for which a NW Pacific origin is not contested, these are predominantly present in the NE Atlantic, with the notable but not surprising exception of the Mediterranean lagoon system (Thau, Venice), and spread relatively little in the Mediterranean. Furthermore, most cells in the Mediterranean Sea, for which species native to NW Pacific have been reported, only contain one species with that origin.

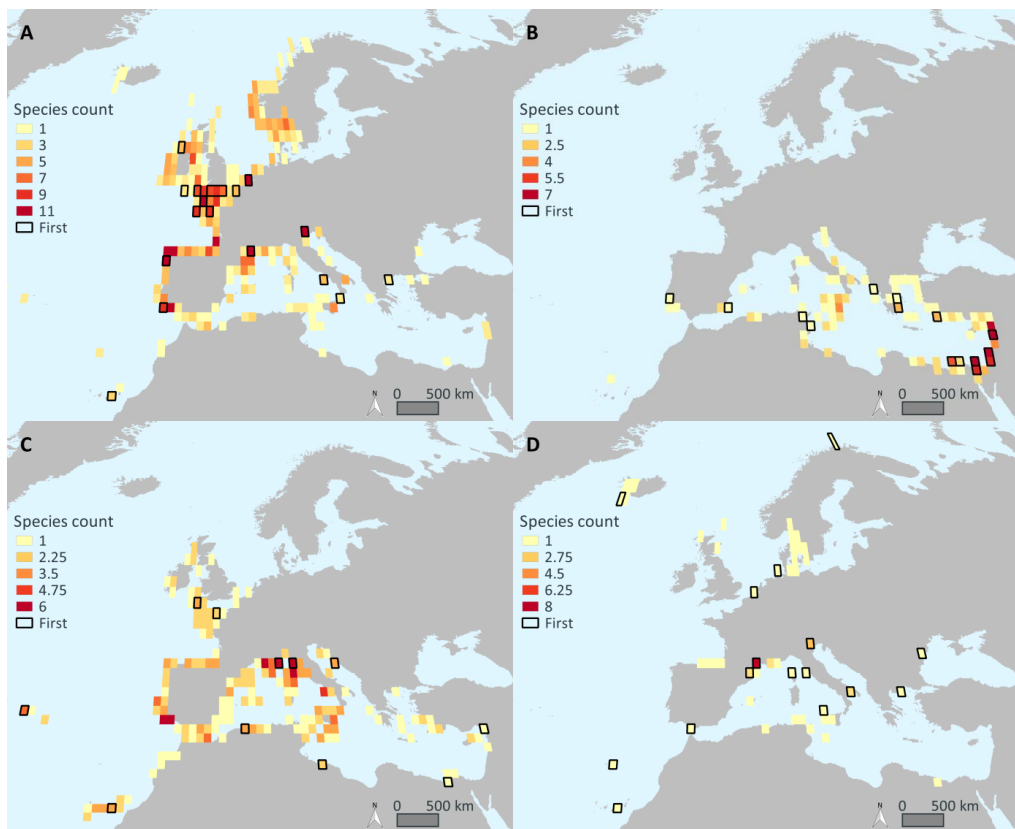


Figure 6. Number of species found in 100 km² grid cells split up by species origin: Northwest Pacific (A), Lessepsian (B), Australasia (C) and Northeast and Western Atlantic (D). Cells containing the first record of one or more species are outlined in black.

In contrast, 34 species with a Lessepsian origin are predominantly distributed in the Eastern Mediterranean Sea with a minority permeating into the Western Mediterranean Sea (Fig. 6B). In contrast 11 species with presumed Australasian origin are predominantly restricted to the Western Mediterranean Sea, Macaronesia and the Atlantic coasts of the Iberian peninsula. Species with Australasian origin appear virtually absent north of Brittany, France. Despite this pattern the introduction vectors for this category of species remains the most elusive. For *Acrothamnion preissii* and *Womersleyella setacea* ship traffic has been suggested as vector based on their first observation close to a major harbour (Livorno, Italy), but accidental release from aquaria is also a possibility (Verlaque et al. 2015). Complicating identification of vectors even further, molecular studies on several nonindigenous species have unveiled multiple independent introductions possibly involving different vectors (McIvor et al., 2001; Provan et al., 2004).

Based on the cumulative plots of the number of species for the most prevalent origins (Fig. 7), we see different patterns depending on the origin of the species. For the NW Pacific we see a sharp increase in the number of first reports around 1970 which slows down after the 1990's. After a big jump in the introduction of species with a Lessepsian origin around 1950, the number of newly reported introduced species has slowly but steadily increased. For the species with an Australasian origin we see that a smaller number of species is being introduced.

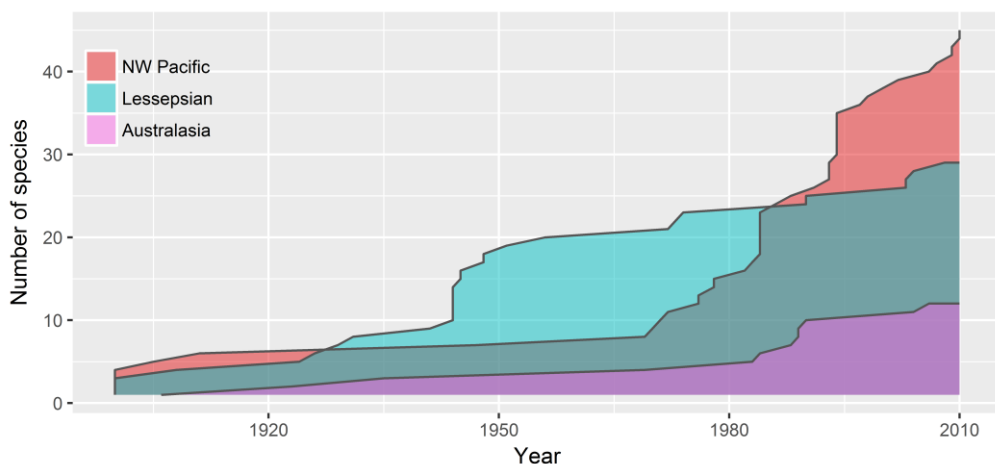


Figure 7. Superimposed cumulative plot of the number of introduced species through time for the most prevalent origins: Northwest Pacific (red), Lessepsian (blue) and Australasia (purple). Only species with a high degree of confidence in their origin are included in this plot.

Conclusion

Detailed analyses of spatial and temporal trends of nonindigenous seaweeds in Europe reveal a complex pattern which can be best understood in terms of the native regions of the species and associated vectors. We identified three different native regions which are responsible for the majority of the nonindigenous species in Europe, the NW Pacific, Australasia and the tropical Indo-Pacific Ocean. Distribution maps of first introductions reveal a non-random pattern with NW Pacific species predominantly introduced in the NE Atlantic region and in lagoon systems in the Mediterranean Sea (Thau and Venice lagoon). Analyses of all distribution records reveal that these species generally do not spread widely in the Mediterranean Sea, but secondary introductions, aided by shellfish transfers from the Atlantic to the Mediterranean lagoon systems and vice versa, are commonly observed. Tropical Indo-Pacific species, predominantly introduced in the Eastern Mediterranean Sea through the Suez Canal remain largely restricted to the latter region with a minority of species spreading to the Western Mediterranean Sea. These species are virtually absent from the Atlantic coasts. The distribution of Lessepsian species likely reflects the environmental tolerance of species with tropical affinities, although one cannot rule out that their current ranges may still expand westward in the Western Mediterranean basin or even Atlantic coasts. Regardless, the distribution of Lessepsian species contrasts to species with Australasian origin who are much more scattered over the entire Mediterranean Sea. Interestingly, Australasian species cannot be easily linked to a specific vector. Fouling, ballast waters and aquarium escapees have all been suggested as vectors (Verlaque et al., 2015). Perhaps the possibility that multiple vectors are involved in the introduction of Australasian species results in the erratic pattern of first reports.

Trends of first reports since 1950 demonstrate that the overall rate of introductions of nonindigenous species is slowing down in Europe. Here we discuss the plausibility of several non-mutually exclusive explanations that could account for the observed decrease in the rate of seaweed introduction in Europe. The most intuitive and optimistic explanation would be that indeed less species have become introduced in Europe during the last two decades. In other words, the measures taken by local and European governments to reduce the influx of nonindigenous species prove effective. The fact that the decline can be attributed primarily to NW Pacific algae (Fig. 7), would corroborate this hypothesis. Livestock transfer of shellfish, the primary vector of algae with a NW Pacific origin, is in principle easier to control compared Lessepsian migration. However, a decline in the rate of reported nonindigenous species doesn't necessarily imply a decrease in introduction rate. Relationships between

introductions and reports of introductions are unfortunately more complicated (Costello & Solow 2003). From the data at hand we can rule out that less attention by the scientific community underlies the decrease in first reports. At least up to the year 2000 the number of records, publication and individual authors showed no sign of decline, while the rate of first reports dropped since 1990. However, it remains possible that a lack of attention in the early second half of the 20th century resulted in a large pool of nonindigenous species waiting to be discovered. If so, the high rates of reports from 1970-1990 could reflect increased scientific interest more than they would reflect introduction rates. The base rate of introductions may have remained constant since 1950, and the pattern of first reports simply reflect a combination of the ease to recognize them and the incentive to report them. A lack of systematic surveys across Europe precludes one from ruling out this scenario. However, there are some indirect indications that introductions rates have not remained constant over the last 50-70 years. Most convincingly, Mineur et al. (2014) correlated Japanese oyster production and disease outbreaks to reports of introduced species in Europe. In addition the difference between Lessepsian and Australasian species which display more constant rates of first reports compared to NW Pacific species is difficult to explain under a constant introduction rate. There is no reason why NW Pacific species would be easier to detect or vice versa.

The observation that at least one source of introductions of marine species in Europe can be controlled, contrasts to the global pattern reported by Seebens et al. (2017) who report an increase across taxonomic groups and geographic regions. Given that livestock transfer of shellfish is the principal vector for the introduction NW Pacific species, it appears that European directives which authorize all movements inside Europe and restrict shellfish stock imports from outside Europe successfully mitigate the influx of nonindigenous species.

While compiling the list of nonindigenous species in Europe, it was quite surprising to encounter so much uncertainty in the primary data at several levels. First, there is taxonomic uncertainty which is rife across the entire geographic region but perhaps even more common in the Mediterranean Sea and Macaronesia. Second, there is also uncertainty as to whether a species is native or introduced in Europe. Both types of uncertainty can be linked but this is not necessarily the case. It is for example possible that a certain species is introduced beyond reasonable doubt, but that the taxonomy is not developed enough to attach a species name. Vice versa, there can be uncertainty on the introduced nature of certain species, despite stable taxonomy. Given this, our final nonindigenous species list should be interpreted with care and we acknowledge that several aspects of the data (e.g. xenoticty) are subjective to some

extent and open for interpretation. Future efforts should be directed toward establishing a DNA-based reference system including European species as well as species from the NW Pacific, Red Sea and other likely donor regions. Reducing the uncertainty in the primary data will be beneficial towards future management of introduced species.

Acknowledgements

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Supporting information

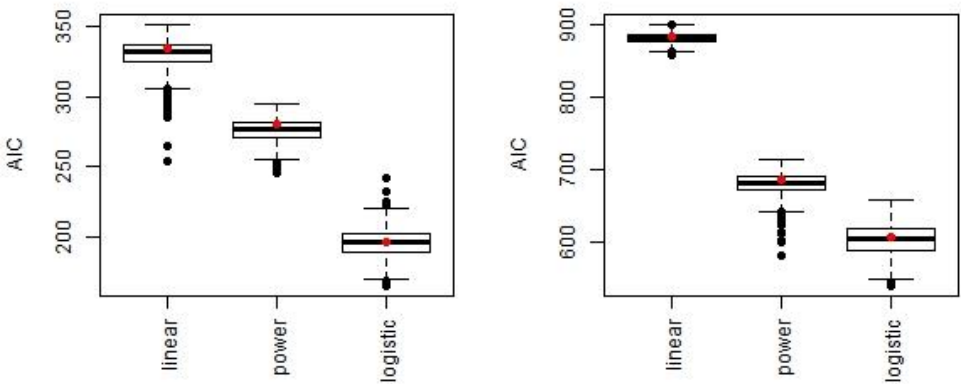


Figure S1. Boxplot of bootstrapped AIC values for curve fitting of the number of introduced species reported for the first time in Europe between 1950 and 2010 (left) and for the number of reported distribution records over all introduced species in the same area and period (right). The fitted curves are a linear curve, a power curve and a logistic curve.

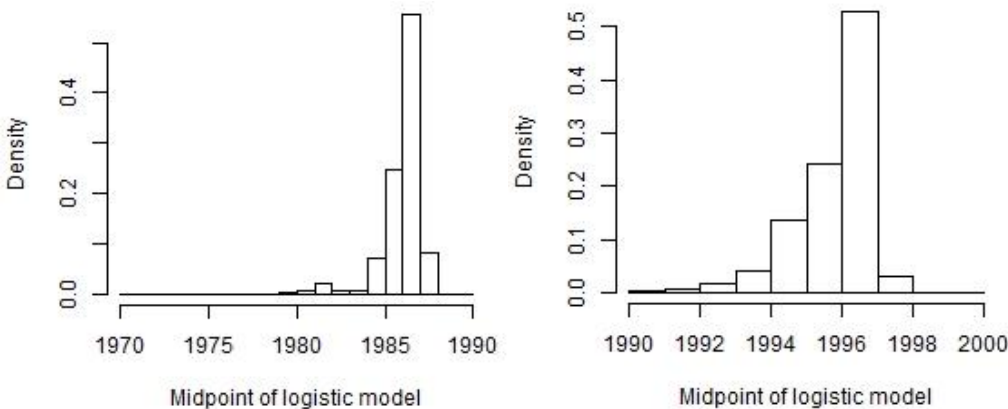


Figure S2. Histograms of the midpoint of the logistic model from 1000 bootstrap samples for the number of introduced species reported for the first time in Europe between 1950 and 2010 (left) and for the number of reported distribution records over all introduced species in the same area and period (right).