

Supporting Information

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SI Text

The application of mathematical models always necessitates dealing with a number of assumptions of a simplified world. The basic model applied here was extensively tested in a sensitivity analysis provided in ref. 10, including a test of various model versions, variation of selected parameters, and discussion of major assumptions. We therefore focused our sensitivity analysis here on the application of the model rather than the basic structure and parameterization. To test the robustness of model predictions, we did the following:

- i) To determine the ecological niche of species more precisely, additional environmental parameters of nutrient concentrations for phosphate, nitrate, and silicate were added to the model in Eq. 2. The widths of the ecological niches expressed by σ were set to approximately the SD of the respective parameter values observed for all ports reported in our database.
- ii) Instead of using constant widths of the ecological niche for all species, σ_T and σ_S were taken as the SD of the temperature and salinity means of the native ecoregions.
- iii) The widths of the ecological niche σ_T and σ_S were modified manually.
- iv) Instead of calculating the ecological niche for each species from its respective native ecoregion, we selected temperature and salinity means from all occupied regions provided by CABI, including native and alien ecoregions.
- v) Instead of using the port with the highest invasion probability as the next invaded port, we selected the next two, respectively five, ports with the highest invasion probabilities.
- vi) To analyze the influence of species selection for model validation, we selected random subsets of species (20–90%) and repeatedly ($n = 1,000$) calculated the fraction of correctly predicted ecoregions.

None of these modifications improved the agreement between observed and predicted distributions of species distinctly (Table S1). However, for single species, the model results can change, while applying one of the modified calculations of the ecological niche. The overall robustness to model modifications and the selection of species indicates that the number of species was high

enough to allow a reliable calculation of the average goodness-of-fit of the model (Fig. S2). Hence, the results presented here are robust to variations in model structure and model application.

A limitation of our modeling approach originates in the availability of ship movement data. Although the observed distribution of marine species can be the result of decades-long spreading histories, shipping data are only available recently and were assumed to be constant in time. Particularly, spreading processes before 1950 may be less reliably predicted using recent ship movement data. To further analyze whether recent shipping data can be used as a proxy to characterize the historic spread of marine alien species, we need to know when spreading dynamics of those alien species considered here were most intense. For example, if species mostly spread in the 19th century, the ship movement data are far less reliable predictors for alien species spread compared with those that occurred in the late 20th century.

We therefore compiled a list of the years of first records of the alien species in a region from online databases and the literature. These first records were reported for countries and large islands, and we decided to not transform them to marine ecoregions because it was not possible to determine the respective ecoregion if the countries/islands bordered more than one ecoregion. For 38 of the 40 alien species used for model validation, we obtained the year of first record for a total of 312 regions (Table S3), but the first records were not available for the full alien ranges. The years of first records ranged from 1693 to 2014 and were highly skewed toward recent times with a median first record of 1986. This means that 50% of all invasions were recorded in recent decades and 79% after 1945. Thus, the majority of invasions happened within the last decades. Ship movement data are only available during 2007–2008. However, major changes in global shipping dynamics occurred much earlier than 1986 with the Suez Canal opening in 1869, the Panama Canal opening in 1914, and the start of containerized transportation in 1956. Thus, the routes of shipping should not have changed distinctly in recent decades, but the distribution of the intensity of shipping has changed particularly due to the rise of the emerging economies. The ship movements before the rise of these countries are not reflected in our dataset. The quality of our model predictions may therefore be higher if historical ship movement could be considered.

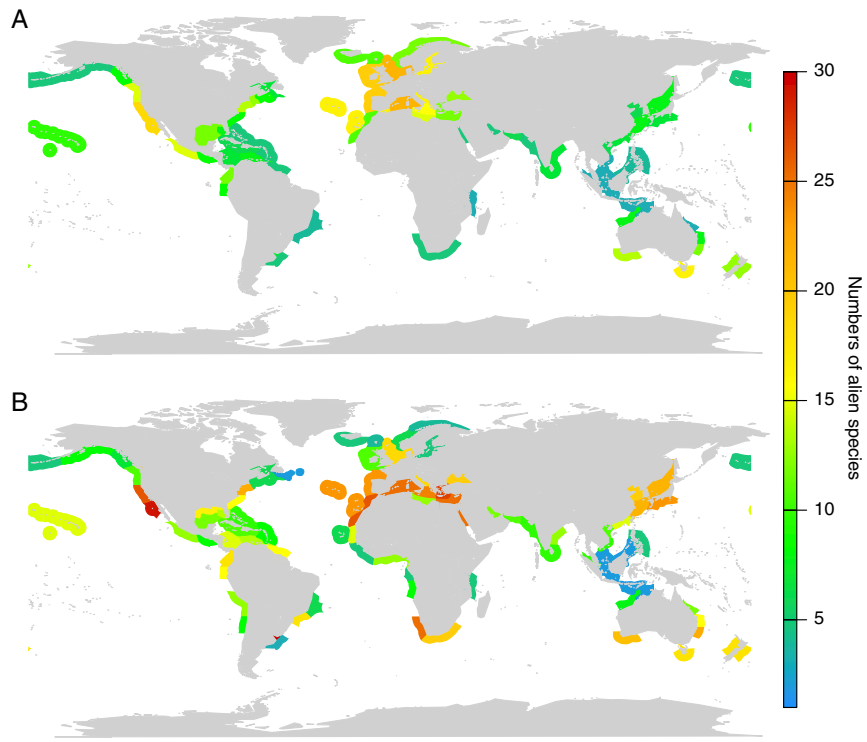


Fig. S1. Validation of model results. The figure shows the observed numbers of alien species per marine ecoregions reported in CABI (A) and the numbers of alien species predicted by the model (B). Only those 90 ecoregions are shown that have at least one port covered in this study. Even though the model slightly overpredicts alien species ranges, the presence/absence of an alien species was correctly predicted for 77% of marine ecoregions outside the species native range on average.

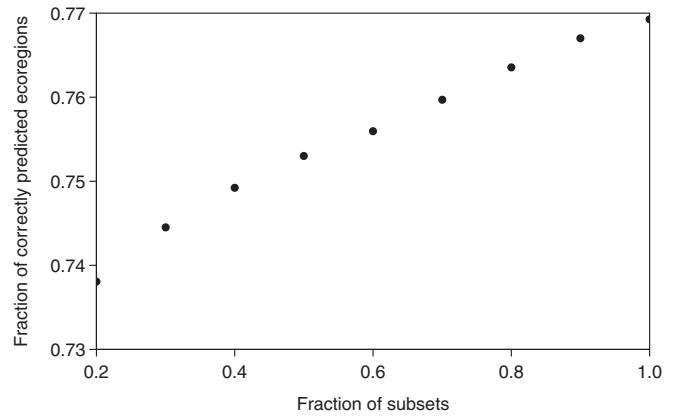


Fig. S2. Influence of selecting random subsets (20–90%) of the 40 species taken from CABI on model accuracy. For each fraction, the random selection was repeated 1,000 times. Model accuracy was expressed as the median of the fraction of corrected predicted ecoregions of all species and averaged for each fraction (*Materials and Methods*). The low variation of the model accuracy (from 77% to about 74%) despite a strong reduction of considered species numbers indicates that the model predictions are mostly independent of the selection of species.

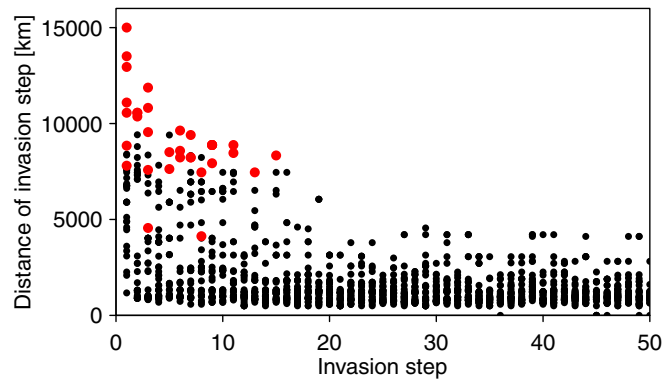


Fig. 53. Geographical distance of invasion steps as a function of the temporal development of the spread for 40 marine species obtained from CABI (dots). The distance of an invasion step was calculated as the great circle distance between the centroids of a newly invaded ecoregion and the nearest already occupied ecoregion. The maximum distance of an invasion step for each species (red dots) was often found among the first invasion steps.

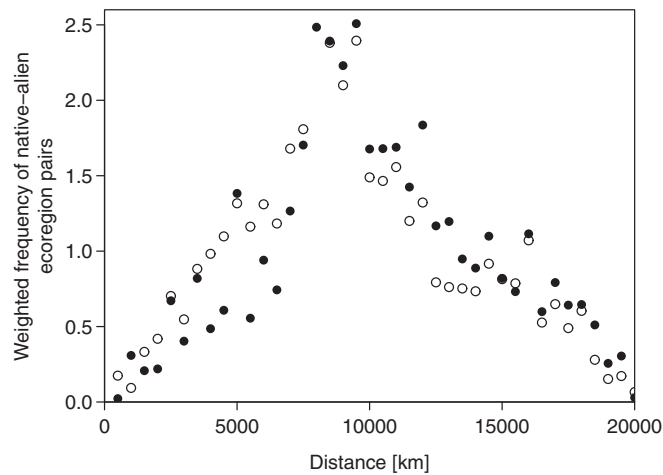


Fig. 54. Weighted frequency of pairs of observed native ecoregions with observed (circles) and predicted (dots) alien ecoregions for 40 marine alien species as a function of the geographical distance between native and alien ecoregion. The weighted frequencies were calculated by determining the distance between the centroids of all native and alien ecoregions weighted by the number of native–alien ecoregions pairs for each species. The weights were summed for each 500-km bin from 0 to 20,000 km to obtain the frequency of links for each bin. The weighting was done to ensure that all species contributed equally.

Table S1. Results of the sensitivity analysis

Model version/ parameterization	Description	Fraction of correctly predicted ecoregions	Statistic
$\sigma_T = 2$; $\sigma_S = 6$	Modifying widths of ecological niche	0.78	0.5
Phosphate	Including nutrient concentration to determine environmental niche	0.77	0.51
$\sigma_T = 2$; $\sigma_S = 10$	Original model parameterization/structure	0.77	0.51
Two ports	Assuming next two ports as being occupied after one simulation step	0.77	0.5
$\sigma_T = 2$; $\sigma_S = 8$	Modifying widths of ecological niche	0.77	0.5
Five ports	Assuming next five ports as being occupied after one simulation step	0.77	0.49
$\sigma_T = 1$; $\sigma_S = 10$	Modifying widths of ecological niche	0.77	0.4
$\sigma_T = 3$; $\sigma_S = 6$	Modifying widths of ecological niche	0.76	0.59
$\sigma_T = 3$; $\sigma_S = 8$	Modifying widths of ecological niche	0.76	0.59
Nitrate	Including nutrient concentration to determine environmental niche	0.76	0.53
$\sigma_T = 1$; $\sigma_S = 6$	Modifying widths of ecological niche	0.76	0.39
All ecoregions	Considering all occupied ecoregions to calculate environmental niche	0.75	0.62
$\sigma_T = 3$; $\sigma_S = 10$	Modifying widths of ecological niche	0.75	0.59
$\sigma_T = 1$; $\sigma_S = 8$	Modifying widths of ecological niche	0.75	0.38
Silicate	Including nutrient concentration to determine environmental niche	0.73	0.54
Variable σ_T and σ_S	Estimating widths of ecological niche from species distribution	0.68	0.52

Several model modifications and parameterizations were tested to analyze their influence on model predictions. The model performance was tested using a goodness-of-fit statistic measured as the fraction of correctly predicted ecoregions to all false predictions [i.e., true positives/(false positives + false negatives)]. The model version applied in this study is highlighted in bold. Note that the model version used in this study is not the best-performing one, to be consistent with the parameterization of ref. 10. The differences to the results of the best-performing model were, however, marginal.

Table S2. The predicted top 10 high-risk species for the North Sea and their associated probability of invasion, $P(Inv)$, in the North Sea

Species name	$P(Inv)$
<i>Symphycloadia marchantioides</i> (Harvey), Falkenberg, 1897	0.0061
<i>Hypnea spinella</i> (C. Agardh), Kützing, 1847	0.0043
<i>Gracilaria tikvahiae</i> , McLachlan, 1979	0.0027
<i>Hypnea cornuta</i> (Kützing), J. Agardh, 1851	0.0024
<i>Ganonema farinosum</i> (J. V. Lamouroux), K. C. Fan and Yung C. Wang, 1974	0.0024
<i>Sargassum fluitans</i> (Børgesen), Børgesen, 1914	0.0019
<i>Prorocentrum minimum</i> (Pavillard), J. Schiller, 1933	0.0019
<i>Polysiphonia harveyi</i> , Bailey, 1848	0.0018
<i>Macrocystis pyrifera</i> (Linnaeus), C. Agardh, 1820	0.0017
<i>Petalonia binghamiae</i> (J. Agardh), K. L. Vinogradova, 1973	0.0010

The two species highlighted in bold are known to have recently established new populations in the North Sea (18, 19).

Table S3. Years of first record of the alien species, which were used for model validation, in a region

Name	Country	Year	Ref.	Name	Country	Year	Ref.
<i>Acanthogobius flavimanus</i>	United States	1963	www.fishbase.org	<i>Littorina littorea</i>	Canada	1840	www.iucngisd.org
	Australia	1971	www.fishbase.org		United States	1879	www.cabi.org/isc
<i>Acentrogobius pflaumi</i>	Australia	1996	39	<i>Marezzelleria neglecta</i>	Belgium	2000	40
<i>Asciadiella aspersa</i>	Argentina	1962	www.iucngisd.org		Denmark	1990	40
	Canada	2012	www.iucngisd.org		United Kingdom	1983	40
<i>Asterias amurensis</i>	Australia	1995	39		Russia	1988	40
	Tasmania	1986	www.cabi.org/isc		Germany	1983	40
<i>Austrominius modestus</i>	South Africa	1949	www.cabi.org/isc		Latvia	1988	40
	The Netherlands	1946	www.corpi.ku.lt/databases/aquanis		Lithuania	1988	40
	Belgium	1950	www.corpi.ku.lt/databases/aquanis		The Netherlands	1983	40
	Denmark	1978	www.corpi.ku.lt/databases/aquanis		Estonia	1991	www.cabi.org/isc
	Germany	1953	www.corpi.ku.lt/databases/aquanis		Finland	1990	www.cabi.org/isc
	Sweden	1939	www.corpi.ku.lt/databases/aquanis		Norway	1990	www.cabi.org/isc
	Ireland	1957	www.corpi.ku.lt/databases/aquanis		Sweden	1985	www.corpi.ku.lt/databases/aquanis
	United Kingdom	1941	www.corpi.ku.lt/databases/aquanis	<i>Microcosmus squamiger</i>	Poland	1986	www.corpi.ku.lt/databases/aquanis
	France	1953	www.corpi.ku.lt/databases/aquanis		Egypt	1919	www.cabi.org/isc
<i>Caprella mutica</i>	Ireland	2003	41		Morocco	1982	www.cabi.org/isc
	Belgium	1998	40		Tunisia	1963	www.cabi.org/isc
	United Kingdom	1991	40		United States	1986	www.cabi.org/isc
	Germany	2004	40		France	1979	www.cabi.org/isc
	The Netherlands	1993	40		Italy	1971	www.cabi.org/isc
	Canada	1997	www.iucngisd.org		Portugal	1992	www.cabi.org/isc
	Norway	1996	www.iucngisd.org		Spain	1978	www.cabi.org/isc
	United States	1973	www.cabi.org/isc		Madeira	2006	www.corpi.ku.lt/databases/aquanis
	New Zealand	2004	www.cabi.org/isc	<i>Mnemiopsis leidyi</i>	Russia	1982	40
	Denmark	2005	www.corpi.ku.lt/databases/aquanis		Germany	2006	40
	France	2004	www.corpi.ku.lt/databases/aquanis		Greece	1990	40
	Spain	2013	www.corpi.ku.lt/databases/aquanis		Italy	1980	40
<i>Carcinus maenas</i>	Argentina	2003	www.iucngisd.org		Romania	1989	40
	Brazil	1857	www.iucngisd.org		Turkey	1991	40
	Canada	1950	www.iucngisd.org		Ukraine	1982	40
	Myanmar	1933	www.cabi.org/isc		Israel	2009	www.iucngisd.org
	Pakistan	1971	www.cabi.org/isc		Norway	2002	www.iucngisd.org
	Egypt	1808	www.cabi.org/isc		Denmark	2005	www.corpi.ku.lt/databases/aquanis
	Madagascar	1922	www.cabi.org/isc		Bulgaria	1986	www.corpi.ku.lt/databases/aquanis
	Panama	1866	www.cabi.org/isc		Georgia	1997	www.corpi.ku.lt/databases/aquanis
<i>Caulerpa racemosa</i> var. <i>cylindracea</i>	Canary Islands	1989	40		Poland	2007	www.corpi.ku.lt/databases/aquanis
	Croatia	2000	40		Sweden	2006	www.corpi.ku.lt/databases/aquanis
	Cyprus	1973	40		The Netherlands	1992	www.corpi.ku.lt/databases/aquanis
	Egypt	1944	40		Belgium	2007	www.corpi.ku.lt/databases/aquanis
	France	1997	40	<i>Musculista senhousia</i>	Israel	1960	40
	Greece	1956	40		Italy	1983	40
	Israel	1955	40		Romania	2002	40
	Italy	1993	40		Mexico	1970	www.iucngisd.org
	Lebanon	1931	40		Canada	1991	www.iucngisd.org
	Malta	1990	40		Australia	1983	39
	Spain	1998	40		Egypt	1964	www.cabi.org/isc
	Syria	1954	40		United States	1924	www.cabi.org/isc
	Tunisia	1926	40		France	1978	www.cabi.org/isc
	Turkey	1980	40		Slovenia	1997	www.cabi.org/isc
	Galapagos	1934	42		Tasmania	1995	www.cabi.org/isc
<i>Charybdis hellerii</i>	Cyprus	1998	40	<i>Mytilus galloprovincialis</i>	New Zealand	1978	www.cabi.org/isc
	Egypt	1933	40		Japan	1932	www.iucngisd.org
	Israel	1924	40		United States	1993	43
				<i>Palaemon elegans</i>	Russia	1939	40
				<i>Palaemon macrodactylus</i>			

Table S3. Cont.

Name	Country	Year	Ref.	Name	Country	Year	Ref.
	Lebanon	1964	40	The Netherlands		1999	40
	Syria	1992	40	Argentina		2000	www.iucngisd.org
	Brazil	1995	www.iucngisd.org	United States		1957	www.cabi.org/fisc
	Colombia	1987	www.iucngisd.org	Belgium		1998	www.cabi.org/fisc
	Cuba	1987	www.iucngisd.org	Bulgaria		2009	www.cabi.org/fisc
	Israel	1924	www.iucngisd.org	France		1998	www.cabi.org/fisc
	Turkey	1981	44	Germany		2004	www.cabi.org/fisc
<i>Ciona intestinalis</i>				Portugal		2004	www.cabi.org/fisc
	Brazil	1958	www.iucngisd.org	Romania		2002	www.cabi.org/fisc
	Canada	1900	www.iucngisd.org	Spain		1999	www.cabi.org/fisc
	Peru	1885	www.iucngisd.org	United Kingdom		1992	www.cabi.org/fisc
	Australia	1958	39	Poland		2014	www.corpi.ku.lt/databases/aquanis
	United States	1917	43	<i>Phyllophiza punctata</i>			
	Hawaiian Islands	1933	45	Israel		1965	40
<i>Crassostrea virginica</i>				Brazil		1955	www.iucngisd.org
	Hawaiian Islands	1866	46	Philippines		1921	www.cabi.org/fisc
	Denmark	1880	40	United States		1981	www.cabi.org/fisc
	United Kingdom	1872	40	Hawaiian Islands		1933	45
	France	1861	40	<i>Polyandrocarpa zorritensis</i>			
	Germany	1887	40	Japan		1991	www.iucngisd.org
	Ireland	1870	www.corpi.ku.lt/databases/aquanis	United States		1994	www.cabi.org/fisc
	Japan	1968	www.cabi.org/fisc	Italy		1974	www.cabi.org/fisc
	United States	1870	www.cabi.org/fisc	<i>Pseudochattonella verruculosa</i>			
	The Netherlands	1939	www.cabi.org/fisc	Denmark		1998	www.corpi.ku.lt/databases/aquanis
	Romania	1973	www.corpi.ku.lt/databases/aquanis	Norway		1998	www.corpi.ku.lt/databases/aquanis
	Belgium	1961	www.corpi.ku.lt/databases/aquanis	<i>Pterois volitans</i>			
<i>Crepidula fornicata</i>				Colombia		2008	www.iucngisd.org
	Belgium	1911	40	Martinique		2011	www.iucngisd.org
	Denmark	1934	40	United States		1985	www.fishbase.org
	France	1949	40	Bermuda		2000	www.fishbase.org
	Germany	1934	40	Anguilla Islands		2010	www.cabi.org/fisc
	Italy	1973	40	Bahamas		1996	www.cabi.org/fisc
	Malta	1973	40	Barbados		2011	www.cabi.org/fisc
	The Netherlands	1929	40	Dominican Rep.		2008	www.cabi.org/fisc
	Norway	1958	www.iucngisd.org	Guadeloupe		2010	www.cabi.org/fisc
	Spain	1983	www.corpi.ku.lt/databases/aquanis	Nicaragua		2009	www.cabi.org/fisc
	Sweden	1948	www.corpi.ku.lt/databases/aquanis	Saint Kitts and Nevis		2010	www.cabi.org/fisc
	Ireland	1893	www.corpi.ku.lt/databases/aquanis	Venezuela		2009	www.cabi.org/fisc
	United Kingdom	1872	www.corpi.ku.lt/databases/aquanis	Puerto Rico		2002	www.fishbase.org
<i>Diplosoma listerianum</i>				Belize		2001	www.fishbase.org
	Canada	2008	www.iucngisd.org	Cuba		2005	www.fishbase.org
	Hawaiian Islands	1900	45	Turks and Caicos		2006	www.fishbase.org
<i>Dreissena polymorpha</i>				Haiti		2007	www.fishbase.org
	Austria	1911	40	Virgin Islands, US		2008	www.fishbase.org
	Belgium	1826	40	Cayman Islands		2008	www.fishbase.org
	Croatia	1995	40	Jamaica		2008	www.fishbase.org
	United Kingdom	1820	40	Costa Rica		2009	www.fishbase.org
	Finland	1995	40	Antigua and Barbuda		2009	www.fishbase.org
	France	1847	40	Panama		2009	www.fishbase.org
	Germany	1824	40	Curacao		2009	www.fishbase.org
	The Netherlands	1826	40	Mexico		2009	www.fishbase.org
	Slovenia	1993	40	Honduras		2009	www.fishbase.org
	Spain	2001	40	<i>Rapana venosa</i>			
	Switzerland	1850	40	United Kingdom		1991	40
	Czech Republic	1890	www.iucngisd.org	Russia		1946	40
	Denmark	1840	www.cabi.org/fisc	France		1998	40
	Canada	1986	www.cabi.org/fisc	Greece		1986	40
	Mexico	1993	www.cabi.org/fisc	Italy		1973	40
	United States	1986	www.cabi.org/fisc	The Netherlands		2005	40
	Belarus	1801	www.cabi.org/fisc	Romania		1961	40
	Estonia	1801	www.cabi.org/fisc	Slovenia		1974	40
	Ireland	1993	www.cabi.org/fisc	Ukraine		1954	40

Table S3. Cont.

Name	Country	Year	Ref.	Name	Country	Year	Ref.
	Italy	1969	www.cabi.org/isc	Israel		2002	www.cabi.org/isc
	Latvia	1801	www.cabi.org/isc	Turkey		1960	www.cabi.org/isc
	Lithuania	1801	www.cabi.org/isc	United States		1998	www.cabi.org/isc
	Poland	1800	www.cabi.org/isc	Argentina		1998	www.cabi.org/isc
	Sweden	1920	www.cabi.org/isc	Uruguay		1998	www.cabi.org/isc
	Russia	1824	www.corpi.ku.lt/databases/aquanis	Spain		2007	www.corpi.ku.lt/databases/aquanis
<i>Ensis directus</i>				Bulgaria		1956	www.corpi.ku.lt/databases/aquanis
	United Kingdom	1989	40	Georgia		1947	www.corpi.ku.lt/databases/aquanis
	Norway	1982	www.iucngisd.org	<i>Rhithropanopeus harrisi</i>			
	France	1991	www.corpi.ku.lt/databases/aquanis		Belgium	1985	40
	Belgium	1986	www.corpi.ku.lt/databases/aquanis		Denmark	1953	40
	The Netherlands	1981	www.corpi.ku.lt/databases/aquanis		Russia	1950	40
	Denmark	1981	www.corpi.ku.lt/databases/aquanis		France	1957	40
	Germany	1979	www.corpi.ku.lt/databases/aquanis		Germany	1936	40
	Sweden	1978	www.corpi.ku.lt/databases/aquanis		United Kingdom	1996	40
<i>Gracilaria salicornia</i>					Italy	1994	40
	Hawaiian Islands	1950	45		Lithuania	2001	40
<i>Grateloupia turuturu</i>					The Netherlands	1874	40
	France	1982	40		Poland	1801	40
	Italy	1969	40		Romania	1951	40
	The Netherlands	1993	40		Spain	1991	40
	Portugal	1998	40		Tunisia	2003	40
	Spain	1990	40		Ukraine	1937	40
	United Kingdom	1973	47		Brazil	1998	www.iucngisd.org
<i>Hemigrapsus sanguineus</i>					Sweden	2014	www.corpi.ku.lt/databases/aquanis
	Tunisia	2003	40		Estonia	2011	www.corpi.ku.lt/databases/aquanis
	United States	1990	www.cabi.org/isc		Latvia	2013	www.corpi.ku.lt/databases/aquanis
	The Netherlands	1999	www.corpi.ku.lt/databases/aquanis		Finland	2009	www.corpi.ku.lt/databases/aquanis
	Germany	2009	www.corpi.ku.lt/databases/aquanis		Bulgaria	1934	www.corpi.ku.lt/databases/aquanis
	Romania	2008	www.corpi.ku.lt/databases/aquanis	<i>Schizoporella errata</i>			
<i>Hemigrapsus takanoi</i>					Canary Islands	2003	40
	The Netherlands	1999	40		Egypt	1977	www.cabi.org/isc
	France	1993	www.cabi.org/isc		Hawaiian Islands	1693	www.cabi.org/isc
	Belgium	2003	www.cabi.org/isc				
	Germany	2007	www.cabi.org/isc	<i>Spartina alterniflora</i>			
	Spain	1997	www.cabi.org/isc		France	1960	40
<i>Hemimysis anomala</i>					Spain	1975	40
	Austria	1998	40		Japan	2001	www.iucngisd.org
	Belgium	1999	40		United Kingdom	1816	47
	Russia	1960	40		Taiwan	2008	48
	France	2000	40		China	1979	49
	Germany	1997	40	<i>Styela plicata</i>			
	The Netherlands	1997	40		Brazil	1883	www.iucngisd.org
	Poland	2002	40		Australia	1966	39
	Ukraine	1955	40		Bermuda	1882	www.cabi.org/isc
	Lithuania	1960	www.cabi.org/isc		United States	1915	43
	Moldova	1969	www.cabi.org/isc	<i>Ulva pertusa</i>			
	Sweden	1995	www.corpi.ku.lt/databases/aquanis		France	1974	40
	Estonia	2009	www.corpi.ku.lt/databases/aquanis		The Netherlands	1993	40
	Finland	1992	www.corpi.ku.lt/databases/aquanis		Spain	1990	www.cabi.org/isc
	Ireland	2007	www.corpi.ku.lt/databases/aquanis				

Regions constitute countries and large islands. Note that only those regions are listed with a known year of first record of the respective species. The full alien ranges of the species are usually larger. For *Ciona savignyi* and *Ulva reticulata*, no first records were found.