



Evaluating the potential of ecological niche modelling as a component in marine non-indigenous species risk assessments



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ABSTRACT

Marine biological invasions have increased with the development of global trading, causing the homogenization of communities and the decline of biodiversity. A main vector is ballast water exchange from shipping. This study evaluates the use of ecological niche modelling (ENM) to predict the spread of 18 non-indigenous species (NIS) along shipping routes and their potential habitat suitability (hot/cold spots) in the Baltic Sea and Northeast Atlantic. Results show that, contrary to current risk assessment methods, temperature and sea ice concentration determine habitat suitability for 61% of species, rather than salinity (11%). We show high habitat suitability for NIS in the Skagerrak and Kattegat, a transitional area for NIS entering or leaving the Baltic Sea. As many cases of NIS introduction in the marine environment are associated with shipping pathways, we explore how ENM can be used to provide valuable information on the potential spread of NIS for ballast water risk assessment.

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1. Introduction

Marine ecosystems are affected by human activities in the sea such as stocking, aquaculture and shipping. These processes often cause invasions of non-indigenous species (NIS) worldwide, alter native communities and lead to the global decline of biodiversity. Frazier et al. (2013) described the invasion of NIS as one of the major environmental stressors for marine ecosystems, which often results in broad economic and ecological damage. Examples of severe invasions with socio-economic consequences are problems in water management systems following mass settlement of the European zebra mussel *Dreissena polymorpha* in the United Kingdom (Oreska and Aldridge, 2011) and Canada (Colautti et al., 2006), or the collapse of the fisheries in the Black Sea following the introduction of the western Atlantic comb jelly *Mnemiopsis leidyi* (Knowler and Barbier, 2000).

According to Kaluza et al. (2010), 90% of world trade is carried out by sea, and global shipping is one of the most important transport networks. Bulk dry carriers and oil tankers are two examples for large amounts of ballast water exchange across biogeographic

regions, promoting the spread of biological invasions. In a ranked list of the 50 most trafficked ports worldwide, six of the top twenty are located in northern Europe (Kaluza et al., 2010), e.g. Europoort Rotterdam (Netherlands), Antwerp (Belgium), Le Havre (France), Hamburg (Germany), Bremerhaven (Germany) and St. Petersburg (Russia). This makes the region enclosing the North and Baltic Sea one of the most significant potential hot spots for biological invasions worldwide (Drake and Lodge, 2004). In the Baltic Sea, an increase in NIS number during the past century can be correlated with the number of ships entering the region with larger volumes of ballast water (Leppäkoski and Olenin, 2000). Similar patterns were observed from the estuaries of North America (Ruiz et al., 1997), and also in the Mediterranean Sea (Gollasch, 2006).

More than 150 NIS have been reported for the North and the Baltic Sea to date (Gollasch et al., 2009). In Europe, more than 1000 species (Vila et al., 2010) and worldwide around 10,000 are estimated to be in transit with ballast water (Bax et al., 2003). Introduced species are often locally distributed and frequently overlooked in the initial stage, but many of them are able to spread successfully over larger areas, such as *Marenzelleria* spp. (Gollasch and Nehring, 2006) or the Chinese Mitten Crab *Eriocheir sinensis* (Therriault et al., 2008).

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The International Maritime Organization (IMO) recognizes the role of ballast water as a vector for NIS and developed the International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM, 2004; IMO, 2004). This convention states that by 2019 at latest all ships have to comply with the Ballast Water Performance Standard. In situations where ballast water does not pose any risk for the environment, i.e. for certain ships on certain routes, an exemption from the Ballast Water Management Convention (BWM) may be granted on the basis of a risk assessment (RA). Such RAs determine the probability that organisms from the donor port survive in the recipient port, and they are based on three principal methods (IMO, 2007):

- (1) Environmental matching. Here, RAs compare the environmental conditions in the donor and recipient ports, to determine if these are sufficiently different so that any species found in the donor port is unlikely to survive and establish reproductive populations in the recipient port. This RA method is usually based on salinity criteria and requires clear definitions of seawater and freshwater, together with detailed studies on salinity gradients in estuary ports and ballast water uptake in these ports (Dragsund et al., 2005).
- (2) Biogeographic matching. This method compares the distribution of non-native species, and if there are overlapping species in donor and recipient ports, the conditions may be similar enough for more species of the donor port to survive in the recipient region (Pikkarainen, 2010; David et al., 2013a).
- (3) Species-specific RAs. This method considers information about individual species in the donor port and the environmental conditions in the recipient port.

The first generation of non-indigenous species-specific RAs combine biological with environmental parameters, but typically use only salinity data and few occurrence records for a limited number of species (see for example David et al., 2013b). Other studies that include more than one environmental parameter use statistical correlation models for making detailed distribution predictions. But such studies only investigate single species (e.g. Herborg et al., 2007; Ba et al., 2010; Kotta et al., 2013). In the present study, we designed an approach that combines data-access with species distribution modelling methods (SDM) such as ecological niche modelling (ENM) to analyze the habitat suitability of large numbers of species under a wide range of environmental conditions. ENM employs environmental variables associated with occurrence data of a species to predict spatial distribution patterns, using a correlative approach. SDMs have been used in a wide range of contexts in recent years, including policy support, for example in conservation decision making (Schwartz, 2012; Guisan et al., 2013) or marine ecosystem management (Reiss et al., 2014).

Here we investigate 18 non-indigenous species (Table 1) belonging to four different ecological categories (zoobenthos, zooplankton, phytobenthos and phytoplankton) to answer the following questions: (1) Is salinity, the current standard environmental parameter in non-indigenous species RAs, the most important and/or the only factor determining the distribution of the species? (2) Can we identify hot- and cold spots in habitat suitability in the Baltic Sea for a large number of non-indigenous species? (3) Can we use model-based evidence to distinguish between natural versus ship-facilitated spread of non-indigenous species along shipping routes? (4) Finally, how can SDM approaches be integrated into existing ballast water risk assessments?

2. Material and methods

2.1. Study area

The study was carried out in Northern Europe (Fig. 1), a global hot spot for biological invasions (Drake and Lodge, 2004; Kaluza et al., 2010). This study area includes the semi-enclosed Baltic Sea, which differs from the fully marine areas of the North Atlantic and North Sea by a strong salinity gradient from around 30–20 PSU in the Skagerrak, to 20–15 PSU in the Kattegat, down to 10 PSU at the mouth of the Baltic Sea and to nearly freshwater conditions in the Gulf of Finland and the Bothnian Bay. Olenin and Leppäkoski (1999) stated that this relatively young brackish-water body (around 10,000 years old) is mostly open for species that are oligohaline (0.5–5 PSU), mesohaline (5–18 PSU) or euryhaline (adapted to all salinities). An important environmental factor in this area is sea surface temperature, which can become low in the northern and northeastern parts of the Baltic during the winter months (November–April: mean 1–3 °C, 1952–2008) (Feistel et al., 2008). The Bothnian Bay/Sea as well as parts of the Gulf of Finland are often covered with ice for several months of the year.

2.2. Species data

We use the term non-indigenous species to refer to species or subspecies transported intentionally or accidentally by a human mediated vector into habitats outside its native range, natural past or present distribution (ICES, 2005). Invasive species are defined here as NIS that have the ability to spread causing damage to the environment, the economy and health. We selected 18 NIS according to the following criteria: (i) species with native ranges in the Atlantic or the Pacific, (ii) species that have invaded Northern Europe in the last 100 years (Table 1) and (iii) species for which we were able to obtain more than 50 environmentally unique occurrence points (Table 2). In addition, eight of the species have a broad salinity tolerance (Tables 1 and 2, in bold). The species were grouped into four categories, i.e. zoobenthos (ZB), phytobenthos (PB), zooplankton (ZP) and phytoplankton (PP), and all species of a category were modelled using the same environmental parameters. The invasion status of the species (Table 1: unknown, non-established or established) strongly depended on the area of interest (from the DAISIE database, www.europe-aliens.org). All scientific names used in this study conform to the nomenclature of the World Register of Marine Species, WoRMS (Appeltans et al., 2014).

Occurrence points for each species were extracted from GBIF (Global Biodiversity Information Facility; <http://gbif.org>) during June–September 2013 (Supplement A). The taxonomic data refinement workflow (DRW) was used to carefully check the synonyms, download, visualize, filter and integrate occurrence records for all species (Mathew et al., 2014). For many species, numerous distribution records exist in the literature, but these are not digitized. We manually geo-referenced additional occurrence data from these sources (Supplement B). In addition, complementary data sets were obtained from scientific networks and environmental agencies (Supplement C) (Table 1).

2.3. Environmental data

Global marine layers used in our study came from Bio-Oracle (<http://www.bio-oracle.ugent.be/>) with a resolution of 5 arc-minutes (Tyberghein et al., 2012), and were used to study abiotic factors such as annual mean sea surface temperature (SST in °C), mean surface salinity (SSS in PSU) and mean photosynthetically available radiation (PAR in Einstein/m²/day). Those data are built

Table 1

Overview of species included in this study, their invasion pathways (A = aquaculture; S = shipping; ST = stocking; U = unknown) and invasion status (unknown; NE = not established; ES = established). Species in bold have a broad salinity tolerance from <5 PSU to >30 PSU. Salinity is shown as M = marine, B = brackish, F = freshwater. Species were grouped into four categories: ZB = Zoobenthos, ZP = Zooplankton, PB = Phytobenthos, PP = Phytoplankton. (GBIF = Global Biodiversity Information facility [database: www.gbif.org], LLUR = State Agency for Agriculture, Environment and Rural Areas, LUNG = State Agency for Environment, Nature Conservation and Geology Mecklenburg-Western Pomerania, SMHI = Swedish Meteorological and Hydrological Institute [database SHARK: Swedish Ocean Achieve: <http://sharkweb.smhi.se>] available through the Swedish Life Watch portal (www.svenskalifewatch.se/en/tools)).

Species, authors	Category	Origin	Invasion path/ status	Introduction/first observation		Salinity	Total # of records	References of occurrence data (>22,000)
				North Sea	Baltic Sea			
<i>Austrominius modestus</i> (Darwin, 1854)	ZB	S Pacific	S/NE-ES	1953	–	M	709	GBIF (709)
<i>Crassostrea gigas</i> (Thunberg, 1793)	ZB	NW Pacific	A, ST/ES	1991	1980s	M	967	GBIF (967)
<i>Ensis directus</i> (Conrad, 1843)	ZB	NW Atlantic	S/ES	1978/79	1981/1993	M, B	817	GBIF (807), Thomsen et al. (2009) (5), www.frammandearter.se (1), own observations (4)
<i>Eriocheir sinensis</i> H. Milne Edwards, 1853	ZB	NW Pacific	S/NE-ES	1915	1926/1932	M, B, F	740	GBIF (613), Drotz et al. (2010) (46), Normant et al. (2000) (8), Ojaveer et al. (2011) (1), Ojaveer et al. (2007) (68), Otto and Brandis (2011) (4)
<i>Gammarus tigrinus</i> Sexton, 1939	ZB	NW Atlantic	ST/NE-ES	1965	1975/1985	M, B, F	1648	GBIF (1566), Berezina (2007) (2), Guszka 1999 (44), Jazdzewski et al. (2004) (6), Kotta et al. (2013) (26), Strode et al. (2013) (4)
<i>Marenzelleria viridis</i> (Verrill, 1873)	ZB	NW Atlantic	S/ES	1983	2004	M, B	789	GBIF (718), Andrulewicz (1997) (4), Bastrop and Blank (2006) (3), Gruszka (1999) (43), Thomsen et al. (2009) (18), Zettler (1996) (3)
<i>Mytilopsis leucophaeata</i> (Conrad, 1831)	ZB	NW Atlantic	S/unknown	1835/ <1994	1930s/<1994/ 2000	M, B, F	268	GBIF (258), Dziubinska (2011) (1), Laine et al. (2006) (5), Verween et al. (2005) (1), Darr and Zettler (2000) (2), www.frammandearter.se (1)
<i>Pilumnus hirtellus</i> (Linnaeus, 1761)	ZB	NW Atlantic	S/unknown	–	2004	M	1270	GBIF (1258), Berggren (2012) (10), www.frammandearter.se (2)
<i>Potamopyrgus antipodarum</i> (J.E. Gray, 1843)	ZB	S Pacific	S/ES	1927	1887/1908	M, B, F	990	GBIF (990)
<i>Rhithropanopeus harrisi</i> (Gould, 1841)	ZB	NW Atlantic	S/NE-ES	<1977	1936/1951	M, B, F	520	GBIF (449), Fowler et al. (2013) (59), Hegele-Drywa and Normant (2009) (4), Kotta and Ojaveer (2012) (8)
<i>Urosalpinx cinerea</i> (Say, 1822)	ZB	NW Atlantic	U/NE-ES	–	1960	M	597	GBIF (597)
<i>Acartia tonsa</i> Dana, 1849	ZP	Indo-Pacific/ Atlantic	S/ES	1916	1925/1934	M, B, F	3939	GBIF (2265), SMHI (1639), Brylinski (1981) (9), Arndt and Schnese (1986) (1), Baretta and Malchaert (1988) (3), Katajisto et al. (1998) (2), Tackx et al. (2004) (5), Wolff (2005) (4), Feike and Heerkloss (2008) (1), Schilau et al. (2011) (4), Drillet et al. (2011) (3), Beaulieu et al. (2013) (1), Cervetto et al. (1995) (1), Leandro et al. (2013) (1)
<i>Mnemiopsis leidyi</i> A. Agassiz, 1865	ZP	Atlantic	S/unknown-ES	2002	2005	M, B	119	GBIF (6), SMHI (8), Faasse and Bayha (2006) (12), Haslob et al. (2007) (7), Janas and Zgrundo (2007) (13), Kube et al. (2007) (7), Oliveira (2007) (6), Javidpour et al. (2009) (1), Fuentes et al. (2010) (9), Mianzan et al. (2010) (4), Reusch et al. (2010) (10), Hamer et al. (2011) (1), Schaber et al. (2011) (4), van Ginderdeuren et al. (2012) (11), Beaulieu et al. (2013) (15), Haraldsson et al. (2013) (5)
<i>Bonnemaisonia hamifera</i> Hariot, 1891	PB	N Pacific	A, S/NE-SE	<1959	–	M	3656	GBIF (3656)
<i>Fucus evanescens</i> C. Agardh, 1820	PB	NW AtlanticN Pacific	S/unknown-ES	–	1989	M, B	526	GBIF (526)
<i>Sargassum muticum</i> (Yendo) Fensholt, 1955	PB	N Pacific	A/ES	1988	–	M, B	1910	GBIF (1910)
<i>Coscinodiscus wailesii</i> Gran & Angst, 1931	PP	Indo-Pacific	A/unknown-ES	1977	1977	M	4042	GBIF (4042)
<i>Proocentrum cordatum</i> (Ostenfeld) Dodge (1975)	PP	NW Atlantic	S/unknown-ES	–	<1999	M, B	2423	GBIF (1190), German monitoring data LLUR and LUNG (319), SMHI (598)

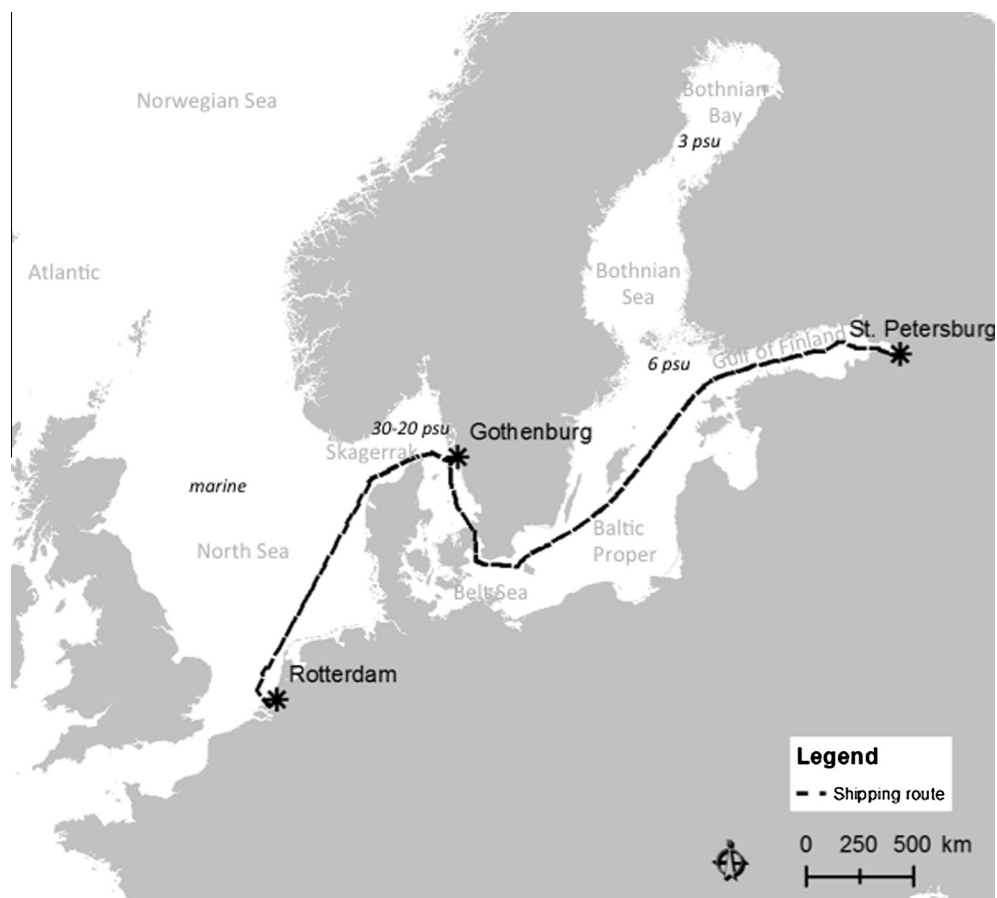


Fig. 1. Map of the study area (North East Atlantic), including hydrographic and biogeographic regions, salinity, main ports, and major shipping routes into the Baltic Sea.

on monthly satellite data (Aqua-MODIS and SeaWiFS; <http://oceancolor.gsfc.nasa.gov/>) and *in situ* measured oceanographic data from the World Ocean Database 2009 (Boyer et al., 2009). The 5 arc-minutes layers for nitrate [NO_3] [$\text{NO}_3 + \text{NO}_2$] concentrations came from the World Ocean Database 2009. The data used were standard level data for surface taken between 1920 and 2008.

Additional marine layers used in our analyses came from AquaMaps (<http://www.aquamaps.org/download/main.php>) with a resolution of 30 arc-minutes (Kaschner et al., 2010). The data set of AquaMaps is built on long-term averages of temporally varying environmental variables. We used sea ice concentration 'SIC' (Ready et al., 2010). The data set also contains geography layers such as distance to land (DL in km) and maximum depth (MD in m), which are important factors for coastal species. The ecological requirements of the species, which were investigated in this study, have been determined from literature (Table 2).

2.4. Analysis

In this study, ENM refers to the estimation of different niches carried out via the estimation of abiotically suitable conditions from observations of the presence of a species, from which the potential distribution area can be derived. In contrast, SDM refers to a wider number of methods regarding the application of niche theory to answer questions about the real distribution of a species in the present, including e.g. biotic interactions and dispersal limitations (Peterson et al., 2011; Reiss et al., 2014).

The analyses were based on four open-source computational pipelines developed through the BioVeL project (www.biovel.eu). All analytical workflows were executed on the BioVeL portal

<http://portal.biovel.eu>. Detailed documentation and tutorials can be found at <https://wiki.biovel.eu/>.

The BioClim workflow (<http://purl.ox.ac.uk/workflow/myexp-3725.2>) was used to retrieve environmentally unique points (Nix, 1986) from a species occurrence file under a given set of environmental layers (Table 2). It also calculates environmental envelopes with the range of the environmental variables (min–max) for a given species (Table 2). The workflow can be executed in batch mode (called data sweep function), using the same parameter settings across a large number of individual input files (i.e. one batch run was created for all species in the same ecological category).

A preliminary correlation analysis of the environmental layers using ENMTOOLS v1.4 (<http://enmtools.blogspot.co.uk>, Warren et al., 2010) showed a Pearson correlation of $r < |0.8|$ for all layers except PAR (data not shown). We performed a jackknife analysis without the PAR variable (Peterson and Cohoon, 1999) to investigate the effect of each environmental factor on the performance of the model. This procedure executes a series of ecological niche models under the same parameter settings, each time excluding a different environmental layer. The performance of the models was assessed using the AUC (area under the curve) to determine which environmental factor had the largest effect on the distribution of the species. The most influential variable was considered the one that, when not included in the model, produced the lowest assessment value.

For ecological niche modelling (ENM) we used version 20 of the ENM workflow in batch mode (<http://purl.ox.ac.uk/workflow/myexp-3355.20>). For more information on the ENM workflow see Leidenberger et al. (2015). We used the Mahalanobis distance method (Mahalanobis, 1936; Farber and Kadmon, 2003) by means

Table 2
Summary of environmental layers used for model construction and their ranges after the BioClim analysis, and ENM and ESW-STACK statistical results for each species. The species are grouped into four categories: ZB = Zoobenthos, ZP = Zooplankton, PB = Phytozoobenthos, PP = Phytoplankton. n = number of environmentally unique points, abiotic parameters (minimum and maximum values); N = Mean nitrate (micromole/l), PAR = Mean photosynthetically available radiation (Einstein/m²/day), MD = maximum depth (m), DL = distance to land (km), SIC = sea ice cover, SSS = sea surface salinity (PSU), SST = sea surface temperature (°C), + = 5 arc-minutes, * = 30 arc-minutes resolution. All layers are mean annual values, excepted MD. Species shown to have a high salinity tolerance (<6.0 – 38 PSU) by the BioClim analysis are in bold. The ENM statistics show the AUC value and Omission Error (%) for each model. A model is considered useful when the average AUC is ≥ 0.75. Besides the AUC, omission errors were calculated during cross-validation for each species using the lowest presence threshold (LPT).

Species/variables	Category	n	Range of environmental variables selected (BioClim envelopes) (min.-max.)										ENM		Habitat suitability (%)	
			N*	PAR*	MD*	DL*	SIC*	SST*	SSS*	AUC	OE (%)	Coverage	Intensity			
<i>Austrorhynchus modestus</i>	ZB	215	-	-	1-4927	0-916	0-0.12	8.70-20.54	23.42-35.70	0.9480 ± 0.040	1.86	16.71	4.56			
<i>Crassostrea gigas</i>	ZB	288	-	-	2-4973	0-644	0-0.71	-0.03-29.85	18.79-36.72	0.9514 ± 0.042	1.75	26.46	8.70			
<i>Ensis directus</i>	ZB	163	-	-	16-4973	0-644	0-0.13	7.66-27.45	10.29-35.94	0.8966 ± 0.045	2.50	39.84	12.73			
<i>Eriochter sinensis</i>	ZB	189	-	-	1-339	0-279	0-0.37	5.27-14.98	2.20-34.91	0.9172 ± 0.030	1.58	16.93	4.37			
<i>Gammarus tigrinus</i>	ZB	166	-	-	1-227	1-87	0-0.25	6.56-22.34	3.82-35.18	0.9481 ± 0.055	2.43	9.41	3.58			
<i>Marenzelleria viridis</i>	ZB	271	-	-	1-4751	0-479	0-0.63	0.54-27.05	5.21-34.93	0.9670 ± 0.038	2.22	14.07	3.25			
<i>Mytilopsis leucophaea</i>	ZB	77	-	-	1-4103	1-434	0-0.20	6.31-28.09	4.91-36.47	0.9362 ± 0.053	6.43	6.70	0.58			
<i>Pilumnus hirtellus</i>	ZB	523	-	-	0-4927	2-916	0-0.05	3.14-24.27	18.08-39.09	0.9380 ± 0.018	1.34	23.28	6.69			
<i>Potamopyrgus antipodarum</i>	ZB	173	-	-	1-740	0-279	0-0.15	4.20-19.38	5.81-37.51	0.9390 ± 0.036	2.25	12.95	4.07			
<i>Rhithropanopeus harrisi</i>	ZB	139	-	-	1-422	1-133	0-0.15	6.28-28.08	6.00-36.32	0.8949 ± 0.059	1.43	19.65	3.78			
<i>Urosalpinx cinerea</i>	ZB	127	-	-	2-4973	0-644	0-0.44	7.66-29.16	15.32-36.42	0.9485 ± 0.029	3.97	33.44	7.74			
<i>Acartia tonsa</i>	ZP	131	-	-	-	-	0-0.20	6.34-28.22	4.74-37.11	0.6409 ± 0.077	0.77	93.63	21.47			
<i>Mnemiopsis leidyi</i>	ZP	78	-	-	-	-	0-0.11	9.16-19.52	7.29-37.68	0.8748 ± 0.061	2.50	72.90	15.44			
<i>Bonnemaisonia hamifera</i>	PB	609	-	-	1-4973	0-644	0-0.22	4.74-26.97	14.26-37.55	0.9376 ± 0.022	2.13	14.28	4.70			
<i>Fucus evanescens</i>	PB	132	-	-	20.97-36.27	0-137	0-0.73	0.01-12.84	8.82-35.25	0.9316 ± 0.035	3.85	26.49	8.31			
<i>Sargassum muticum</i>	PB	424	-	-	1-4973	0-1593	0-0.06	8.01-26.87	14.88-38.21	0.9355 ± 0.024	1.41	38.66	12.86			
<i>Coccinoidiscus waltlesi</i>	PP	1263	0.12-33.62	24.79-49.34	-	-	0-0.13	4.71-30.03	19.90-36.02	0.8186 ± 0.013	0.79	84.75	46.41			
<i>Proocentrum cordatum</i>	PP	315	0.23-26.74	25.73-49.34	-	-	0-0.64	-0.81 to 28.89	5.64-38.25	0.7236 ± 0.036	1.26	97.15	61.28			

of the openModeller Environmental Distance algorithm (Muñoz et al., 2011). Although not widely used in ENM studies, Mahalanobis distance has some interesting and useful features when compared with other algorithms. Among them is the fact that model shapes produced by this algorithm are n-dimensional ellipsoids, better reflecting the principle of central tendency in niche theory (Farber and Kadmon, 2003) and matching convex representations as hypothesized by Soberón and Nakamura (2009). Additionally, only presence points are required, with no need to generate pseudo-absence or background points, therefore not requiring prior knowledge of the species' origin and dispersal ability for model calibration, according to a recent study (Barve et al., 2011) (see also Leidenberger et al., 2015 for more information). Models were created using each species' maximum distribution range and then projected into the North East Atlantic area. For each species, we ran a single model combining environmental layers with a resolution of 5 and 30 arc-minutes. Models were tested using 10-fold cross-validation based on the AUC value and omission error rate (false negative rate). The results of the ENMs were presented as potential distribution maps (PD maps), showing the suitable habitat of a species in a particular geographic region at a particular time (Muñoz et al., 2011). The sweep function allowed automated batch processing of all species belonging to the same ecological category.

The statistical workflow (ESW-STACK v.3) (<http://purl.ox.ac.uk/workflow/myexp-3856.3>) was used to generate PD maps for each species showing the known distribution (input occurrence points), and calculate summary statistics from the PD maps, such as number of cells (ncell), mean and median value (mean, median), coefficient of variation (cv), standard deviation (sd), current minimal and maximal value (min, max) and number of 'noData' values in the file (countNA). The workflow furthermore allows the computation of cumulated potential species distribution through computation of an average sum layer from the input raster layers. Here, the sum layer is computed for each ecological category as a mean value from all input values in corresponding raster cells (see Table 1 for definition of the categories). Additionally, the ESW-Stack workflow was used to calculate the extent (i.e. coverage) and intensity (%) of suitable habitat in the region of interest for each species. All calculations in this workflow are implementations of the R statistical environment (R Core Team, 2013) using the raster (Hijmans, 2013) and gdal packages (Bivand, 2013) for processing raster files.

2.5. Shipping routes

Non-indigenous species' distributions were analyzed along a central ship traffic route, as in David et al. (2013a). The route starts in Rotterdam (Netherlands) and ends in St. Petersburg (Russia), via Gothenburg (Sweden), the Kattegat, the Baltic Proper and the Gulf of Finland (Fig. 1). A transect plot was created for each ecological category based on the PD maps, showing the potential habitat suitability for each species along the entire shipping route. For zoobenthos (ZB), only species with a broad salinity tolerance were included in the transect plot (Table 1). We would like to note here that although risk of spread for ballast water organisms is concentrated to ports, this could occur anywhere along the shipping route depending on the point of ballast water exchange or in the case of NI biofouling organisms, travelling on ships' hulls.

3. Results

3.1. Analysis of salinity tolerance, environmental parameter analysis

Eight out of eighteen species investigated (44.4%) tolerate a broad salinity range between <6.5 PSU and fully marine waters

Table 3

Results of the jackknife analysis (AUC values) for the different layers (N = Mean nitrate (micromole/l), MD = maximum depth (m), DL = distance to land (km), SIC = sea ice cover, SSS = sea surface salinity (PSU), SST = sea surface temperature (°C)). PAR = Mean photosynthetically available radiation (Einstein/m²/day) was deleted after the correlation analysis. The AUC values in bold indicates the layer with the largest effect on the distribution of the species.

Species/layers	N	MD	DL	SIC	SST	SSS
<i>Austrominius modestus</i>	–	0.9515	0.9528	0.9574	0.9498	0.9573
<i>Crassostrea gigas</i>	–	0.9492	0.9408	0.9262	0.9359	0.9575
<i>Ensis directus</i>	–	0.9119	0.9216	0.9076	0.9070	0.9040
<i>Eriocheir sinensis</i>	–	0.9356	0.9266	0.9326	0.9342	0.9320
<i>Gammarus tigrinus</i>	–	0.9591	0.9584	0.9561	0.9602	0.9564
<i>Marenzelleria viridis</i>	–	0.9754	0.9762	0.9619	0.9758	0.9788
<i>Mytilopsis leucophaeata</i>	–	0.9256	0.9209	0.9449	0.9295	0.9613
<i>Pilumnus hirtellus</i>	–	0.9542	0.9323	0.9343	0.9414	0.9312
<i>Potamopyrgus antipodarum</i>	–	0.9234	0.9318	0.9670	0.9307	0.9502
<i>Rhithropanopeus harrisi</i>	–	0.9128	0.9215	0.9409	0.9076	0.9231
<i>Urosalpinx cinerea</i>	–	0.9410	0.9335	0.9407	0.9378	0.9522
<i>Acartia tonsa</i>	–	–	–	0.6739	0.6227	0.6902
<i>Mnemiopsis leidyi</i>	–	–	–	0.9161	0.5911	0.8871
<i>Bonnemaisonia hamifera</i>	–	0.9531	0.9501	0.9380	0.9415	0.9495
<i>Fucus evanescens</i>	–	0.9399	0.9414	0.9206	0.9181	0.9245
<i>Sargassum muticum</i>	–	0.9403	0.9255	0.9433	0.9305	0.9400
<i>Coscinodiscus wailesii</i>	0.8429	–	–	0.7984	0.6471	0.7852
<i>Prorocentrum cordatum</i>	0.6971	–	–	0.7074	0.6221	0.7640

(Table 2). These species (*Eriocheir sinensis*, *Gammarus tigrinus*, *Marenzelleria viridis*, *Mytilopsis leucophaeata*, *Potamopyrgus antipodarum*, *Rhithropanopeus harrisi*, *Acartia tonsa*, *Prorocentrum cordatum*) are also characterised by a low temperature minimum in the study area (≤ 6.5 °C) (Table 2), implying that they are able to survive in the Baltic Sea.

The jackknife analysis demonstrated that out of the 18 species, only two zoobenthic species (*Ensis directus* and *Pilumnus hirtellus*) have a potential distribution determined by SSS (Table 3). Most of the species' distributions were affected primarily by sea ice concentration (SIC) and sea surface temperature (SST) (61%), rather than by salinity (11%). For 28% of the species, maximum depth (MD) and distance to land (DL), respectively, had the largest effect on the distribution of the species (Table 3).

3.2. Analysis of habitat suitability: hot- and cold spots

Two areas with high habitat suitability (hot spots) could be identified from the analysis (Fig. 2). First, coastal areas of north-western Europe, from northern France to northern Denmark and southern Norway, as well as around the British Isles and southern Iceland (Fig. 2) are particularly suitable for NI zoobenthic, zooplanktonic and phytobenthic species. In contrast, phytoplanktonic species show less habitat suitability along the coasts, especially in the Wadden Sea, the Northern coasts of France, Belgium, the Netherlands, and Germany (Fig. 2). The second hot spot lies in the transition zone between the North Sea and the Baltic Sea, including the Skagerrak, Kattegat and the Belt Sea region (Figs. 2 and 3a–r). All species analyzed showed potential habitat suitability in at least one of these areas, while for at least 11 species the intensity was high in this region (Fig. 3a–r).

In addition to non-indigenous hot spots, we could also identify areas showing low overall habitat suitability (cold spots). These areas are located in the central North Sea and the Bothnian Bay

(Fig. 2). Benthic and planktonic species differ in their coverage and intensity for those cold spots. There are more cold spots for the benthic species, and fewer for planktonic species due to higher coverage values for plankton (Fig. 2).

In the region of interest, the coverage was higher for the pelagic (>73%) than for the benthic (<40%) categories. The intensity only differed slightly (pelagic >15% versus benthic <13%) (Table 2). Phytoplanktonic species, such as *Coscinodiscus wailesii* and *Prorocentrum cordatum* and the zooplanktonic species, *Acartia tonsa* and *Mnemiopsis leidyi*, showed high potential habitat suitability in the North East Atlantic and the Baltic Sea, mainly in the Skagerrak and Kattegat (Table 2, Fig. 3l, m, q, and r). For the phyto-benthic species (*Bonnemaisonia hamifera*, *Fucus evanescens* and *Sargassum muticum*) (Fig. 3n–p) habitat suitability coverage values were in between the phytoplanktonic and zoobenthic species, with a variation of 14–28% (Table 2). For these species the potential for establishment is high in the North East Atlantic, and low for the Baltic Sea in the case of *Fucus evanescens*.

Analysis of individual species' potential distribution patterns shows that zoobenthic species have narrow potential habitats, which cover between 6% and 40% of the investigated region (Table 2, Fig. 3a–k) and show two types of distribution patterns. The first hot spot (the Atlantic cluster) contains species with coastal habitats in the North Sea, the English Channel, and the west coast and/or east coast of the British Isles (*Austrominius modestus*, *Crassostrea gigas*, *Ensis directus*, *Pilumnus hirtellus*, *Urosalpinx cinerea*) (Fig. 3a, b, c, i, and k). These species need salinities higher than 6.5 PSU and/or preferably warmer temperatures to survive (Table 2). The second hot spot (the Baltic cluster) contains species with coastal habitats that span from Belgium to Denmark and into the Baltic Sea (*Eriocheir sinensis*, *Gammarus tigrinus*, *Marenzelleria viridis*, *Mytilopsis leucophaeata*, *Potamopyrgus antipodarum*, *Rhithropanopeus harrisi*) and tolerate lower salinities and lower temperatures (Table 2, Fig. 3d, e, f, g, i, and f) compared to the species of the first cluster.

3.3. Natural-spread versus ship-facilitated invasions

Natural spread can be defined by the suitable habitats along the entire study region, and can be assessed by looking for major gaps in the distribution area (Fig. 3a–r). In addition, transect plots can be useful in the case of species bound to the ship's hull or in the case of NIS picked up or released from the ballast tank along the shipping route. We assume here that ballast water exchange (and thus release of NIS) could happen at any point along the shipping route. The transect plots presented here allow us to determine the habitat suitability between ports and along the shipping route from Rotterdam to Gothenburg and St. Petersburg. These plots show clear differences between the four ecological categories (Fig. 4a–e). Individual PD maps for zoobenthic species (including only species with a high salinity tolerance), show that there is high habitat suitability along the entire distribution area analyzed for most of the species, indicating a high potential for natural dispersal (natural spread) especially for *Eriocheir sinensis* and *Gammarus tigrinus* (Figs. 3d–e and 4a). On the other hand, there are areas showing sudden drops in habitat suitability along the shipping route, as shown on the transect plot (4a). These areas may be due to missing data or zones of unsuitable habitat (e.g. deep water) that the species must cross to spread further. Two of the zoobenthic species extend into the Bothnian Bay and Gulf of Finland (*Eriocheir sinensis* and *Gammarus tigrinus*) (Fig. 3d–e). *Marenzelleria viridis*, *Mytilopsis leucophaeata* and *Rhithropanopeus harrisi* showed suitable habitats into the Bothnian Sea (Fig. 3f–g, and j), whereas the potential distribution of *Potamopyrgus antipodarum* seems to be restricted to the Baltic Proper only (Fig. 3i) (4b). The two zooplanktonic species (*Acartia tonsa*, *Mnemiopsis leidyi*) show no potential distribution

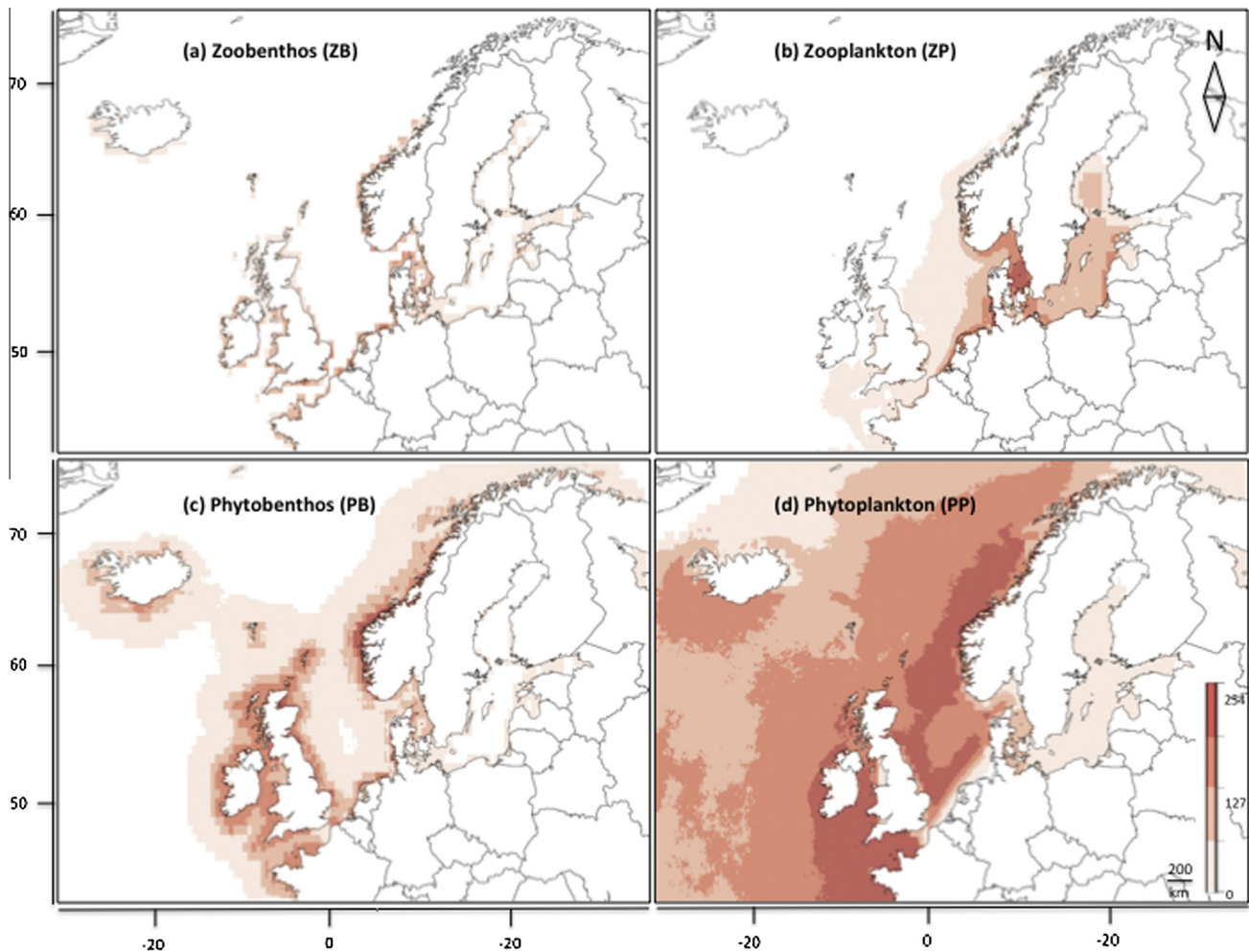


Fig. 2. Potential distribution maps showing the combined invasive potential of all eleven macrozoobenthic species (ZB), two zooplanktonic species (ZP), three phytobenthic species (PB) and two phytoplanktonic species (PP).

further than the Baltic Proper (Fig. 3l and m), while the two remaining categories of phytobenthic and phytoplanktonic species showed high habitat suitability and risk of natural spread only between Rotterdam and Gothenburg on the transect plots (Fig. 4c–e).

The transect plots indicate that at least two species, namely *Fucus evanescens* and *Prorocentrum cordatum* are characterised by high habitat suitability values at the beginning and the end of the Baltic shipping route (Gothenburg – St. Petersburg), but display low habitat suitability values in between (Fig. 4d and e). In this case, dispersal between ports may only be possible through ships carrying these organisms across a larger area of unsuitable habitat.

3.4. Integrating SDMs into non-indigenous species risk assessments

In Table 4, we show how SDMs and related model based evidence can contribute to non-indigenous species RAs. The *BioClim* tool gives a useful overview of the species' range of environmental variables based on data and model based processes (Table 2). The bioclimatic envelopes provide, for instance, knowledge on the salinity tolerance of species from the donor port, but also min-max ranges for other important chosen environmental parameters for the species. The *Jackknife Analysis* can determine the influence of individual environmental parameters for the distribution of the species, which can be important for environmental and biogeographic matching (Table 3). The *Ecological Niche Modeling* covers almost all indicators used in RA (Table 4), with PD maps of each

species analyzed in the area of interest (Fig. 3a–r). The *ENM-STACK* summarizes the coverage and intensity information for a group of species (i.e. an ecological category), and allows identification of hot- and cold spots (Fig. 2) that can inform about potential ballast water exchange sites. The *Statistics* produced present the coverage and intensity of habitat suitability for each species, allowing comparisons and predictions between the donor and recipient ports and between different species (Table 2) (Fig. 3a–r). The *Transect Plots* based on the PD maps can help determine high suitability areas where natural spread can occur as well as major gaps in the distribution area. Moreover, the plots show habitat suitability along a shipping route, important information for ballast water exchange along the route, complementing all three principal methods used in the BMW Convention (Table 4).

4. Discussion

4.1. Analysis of salinity tolerance, environmental parameter analysis

Surprisingly, our study shows that sea surface salinity (SSS) is not the most important factor determining the distribution of the NIS investigated, even for species that are not tolerant to a broad range of salinities (Table 3). This contradicts current practices in non-indigenous species RAs that are typically based on salinity matching of the species (IMO, 2004; Gollasch and David, 2011; David et al., 2013a).

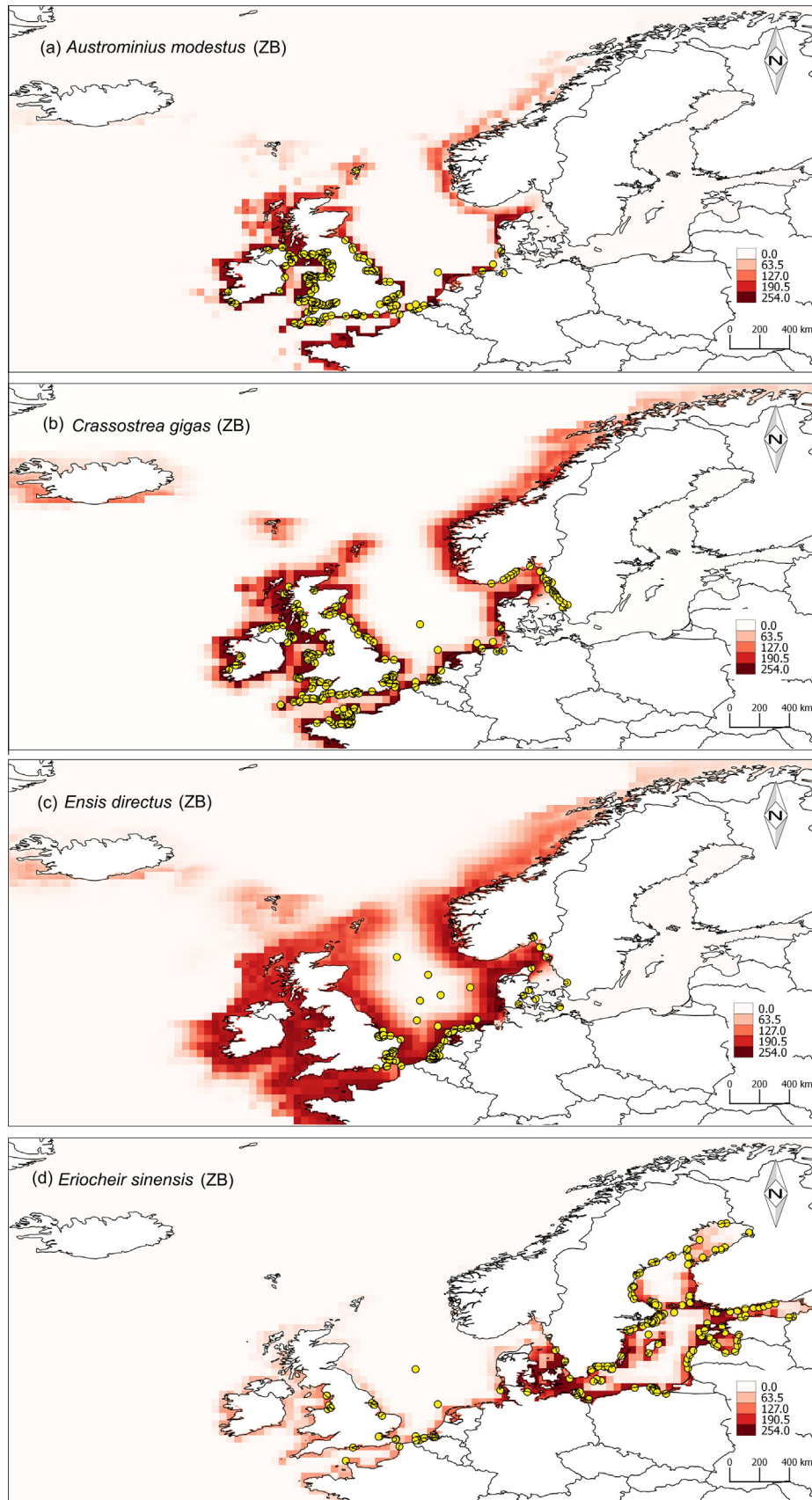


Fig. 3. (a–r) Potential distribution maps presenting habitat suitability with occurrence points (yellow dots) showing the actual distribution for each species. Colour scale indicates habitat suitability, ranging from 0 (unsuitable, in white) to 254 (maximum suitability, in dark red).

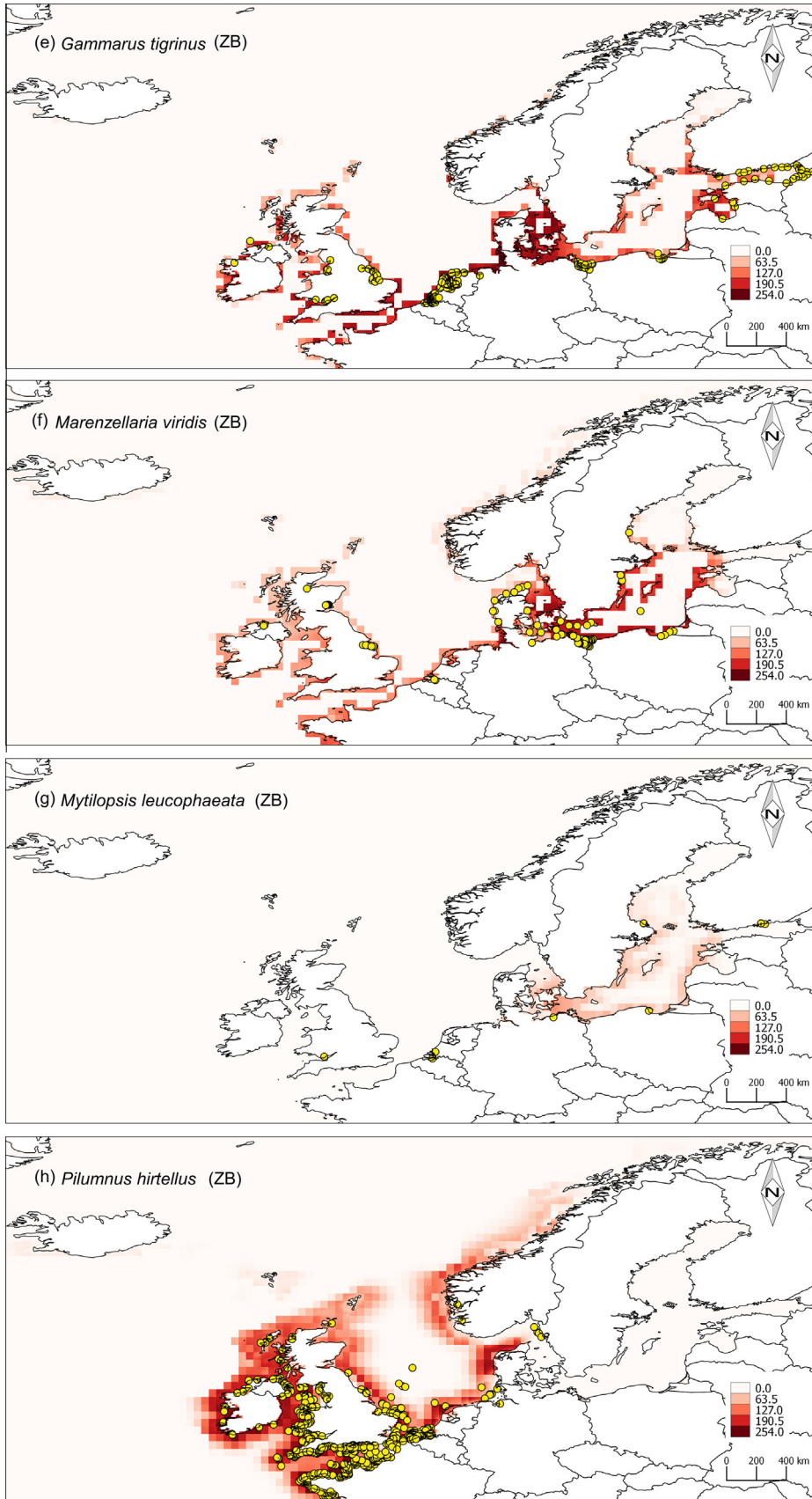


Fig. 3 (continued)

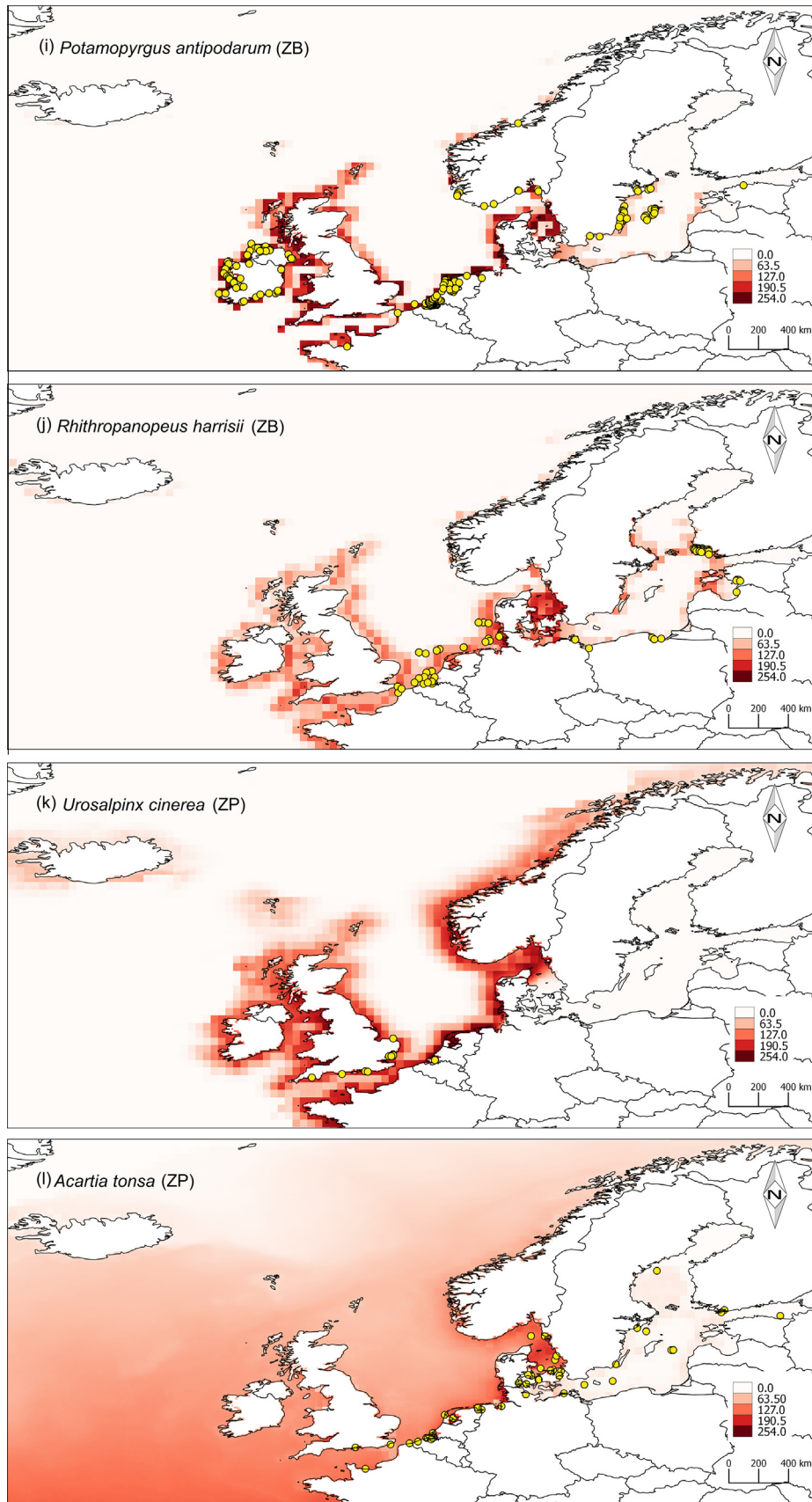


Fig. 3 (continued)

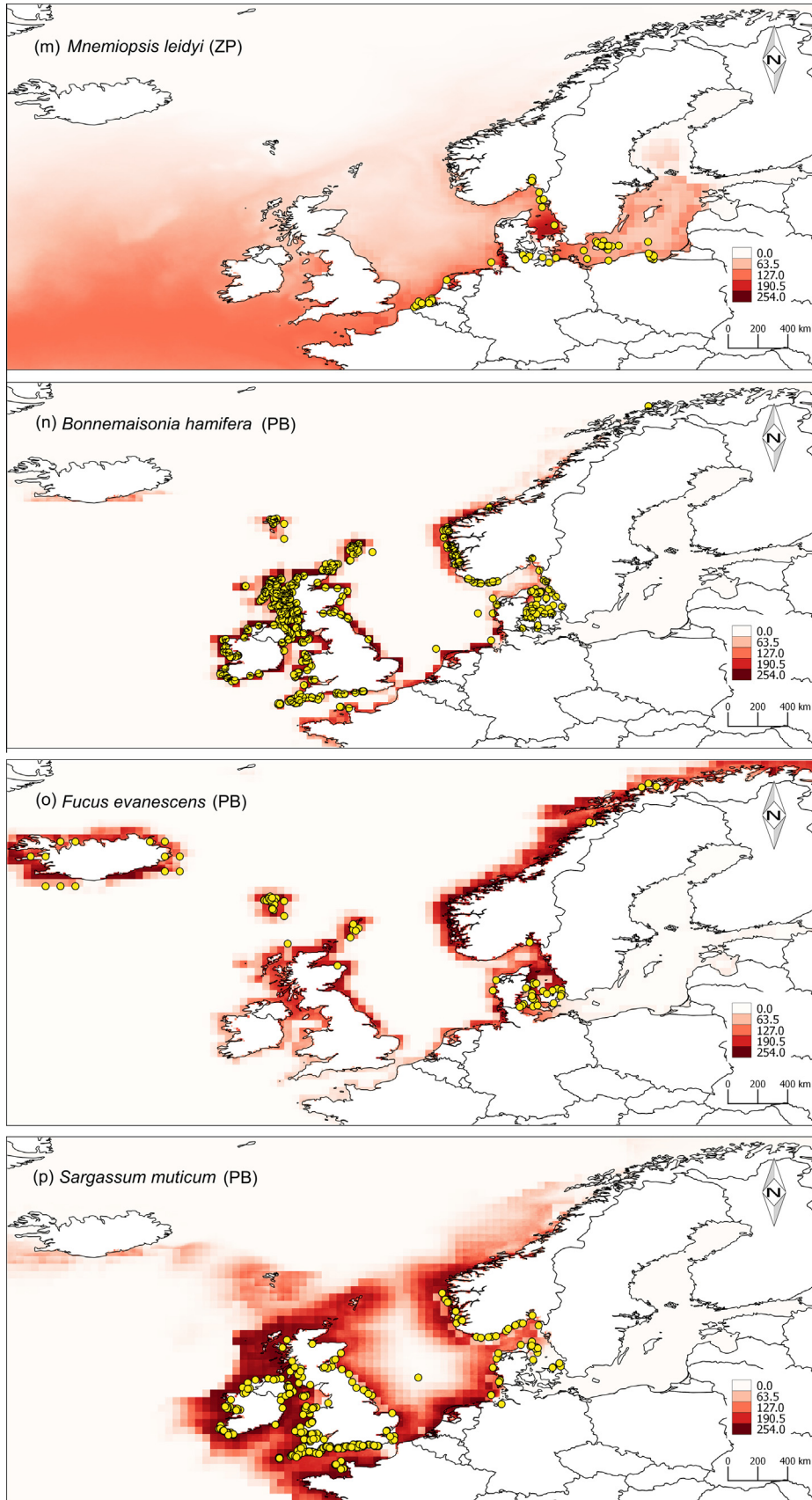


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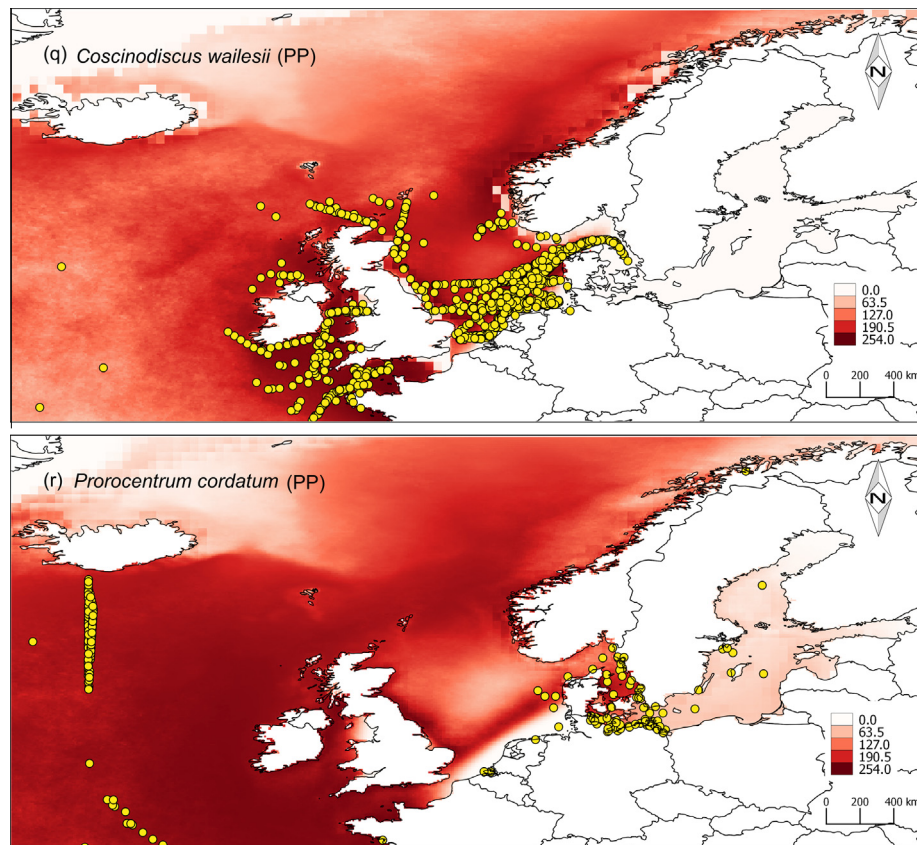


Fig. 3 (continued)

For the Baltic Sea, it is important to consider that SSS varies in contrast to bottom salinity, which is an important environmental factor for benthic organisms. No bottom salinity layers are available at present, which is why this parameter could not be taken into account in our study.

Our results show that sea surface temperature (SST) and sea ice concentration (SIC) determine the habitat suitability in more than 60% of the cases in the area of interest. One reason for this can be that most of the NIS analyzed here have their origins in warmer regions, such as the Southern and Indo-Pacific (e.g. *Austrominius modestus*, *Potamopyrgus antipodarum*, *Acartica tonsa*, *Coscinodiscus walesii*), which explains why several species are not able to overwinter in colder sea areas like the Baltic Sea. At present, low temperatures prevent numerous NIS from establishing in the colder Baltic Sea or Northern Europe, where large areas are covered with ice in winter. But this may change in future (Meier et al., 2012) and ENMs based on future climate models can play an important role in RAs in the future (Jones et al., 2013; Leidenberger et al., 2015), to forecast the effects of climate change on the establishment of NIS.

In the case of *Crassostrea gigas* some occurrences along the Swedish west coast lie outside the predicted suitable habitat (Fig. 3b). Here, the most southern records from the Kattegat and Belt region may not be sustained populations, as suggested by current monitoring programs in the region. Two recent studies observed that the species does not advance from the Kattegat into the Belt region, but instead migrates northeastward along the Norwegian and Faroe coastline under future climate change scenarios (Jones et al., 2013; Laugen et al., 2015). For *U. cinerea* only a few records were available, but the results showed that habitat suitability for this species is high in Northern Europe: along the entire coast from Northern France up to Denmark and Norway, as well as around the British Isles and southern Iceland. For this

species there might be an increased risk of spread in the near future (Fig. 3k).

4.2. Analysis of habitat suitability: hot- and cold spots

In general, the average PD maps for each ecological category show that benthic species have a more restricted potential distribution than pelagic ones (Fig. 2). Habitat suitability differs significantly between the categories (Fig. 2). However, more general patterns are difficult to analyze because only a few planktonic species (four in total) and phyto-benthic species (3 in total) were included in this study. Global hot spots for invasive species have been analyzed before, although only based on worldwide patterns of ship traffic (Drake and Lodge, 2004). Our study shows that the transition zone between the fully marine North Sea waters and the brackish Baltic Sea (Skagerrak, Kattegat and Belt Sea area) is a potential hot spot for invasive species (Figs. 3 and 4) where ballast water exchange should be avoided. It is a highly trafficked area (Drake and Lodge, 2004) acting as sink of invasive species, which, depending on their salinity tolerance and adaptive potential, could either migrate to the North Sea and/or the Baltic Sea. This specific sea area is characterised by short distances to coastlines, including Natura 2000 areas (Andersson, 2007). A study based on oceanographic modelling also confirms that the risk of NIS uptake could be high if ballast water is exchanged in the Norwegian Trench and Skagerrak, and that these areas are not suitable for ballast water exchange (Andersson, 2007).

In our study, ENM results suggest potential cold spots for ballast water exchange, in the middle of the North Sea and in the Bothnian Sea (Fig. 2), but those locations should be tested using oceanographic modelling.

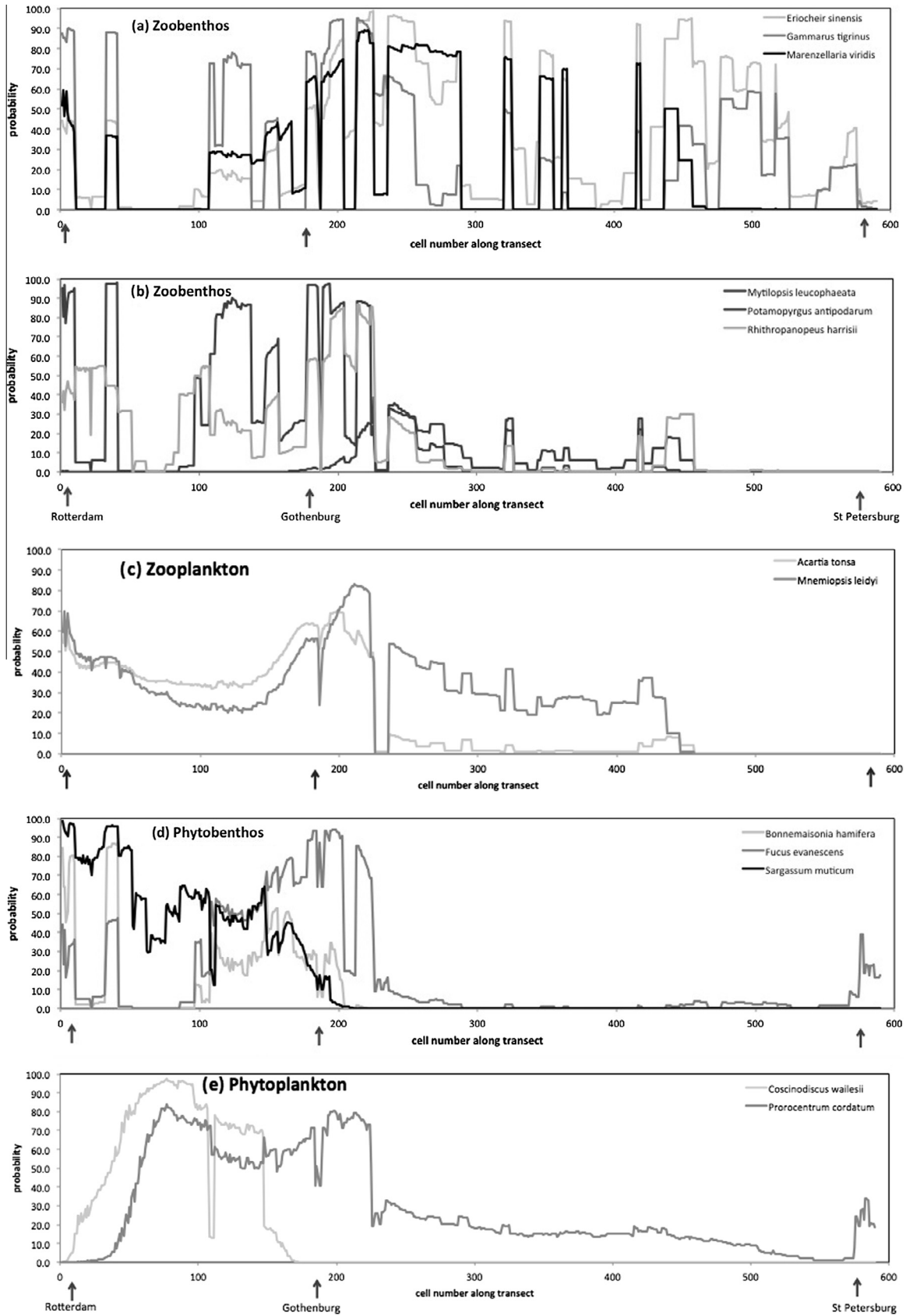


Fig. 4. (a–e) Transect plots for the four species groups (zoobenthos, zooplankton, phytobenthos and phytoplankton) along the shipping route from Rotterdam/Netherlands to Gothenburg/Sweden and St. Petersburg/Russia.

Table 4

Summarizing the use of species distribution modelling (SDM) based methods in marine invasive species risk assessments. Abbreviations: Potential distribution (PD) maps, Ecological niche modelling (ENM) workflow, ENM Statistical Workflow with raster difference computation (ESW DIFF workflow).

Indicators/methods	'Traditional' method	SDM based method	Outputs using SDM	Case study/example	Requirements of SDM based methods
Presence of invasive species in donor or recipient port (occurrence records)	Monitoring in ports, literature surveys, invasive species databases	Geo-referenced occurrence records	Map showing the occurrence points	This study (Fig. 3a–r), David et al. (2013a)	–
Presence of high salinity tolerant species in donor or recipient port	Expert opinion, literature, experimental studies	BioClim algorithm	Range (min–max) and mean of the species (environmental ranges)	This study (Table 2), Reiss et al. (2011), Freshwater: Gallardo et al. (2012) and Boets et al. (2013)	Occurrence records, environmental layers including sea surface salinity
Potential for invasive species from donor port to survive in recipient port	Environmental matching, biogeographic matching	ENM workflow, ESW-STACK workflow	PD map and statistics	David et al. (2013a,b)	Occurrence records, environmental layers
Risk of natural spread from donor to recipient port (dispersal ability)	Expert opinion, analysis of marine currents	ENM workflow, ESW-STACK workflow	PD map and statistics	This study (Figs. 3a–r and 4)	Incorporate dispersal in SDM (Robinson et al., 2011)
Potential distribution of the invasive species (invasive potential)	None	ENM workflow, ESW-STACK workflow	PD map and statistics	This study (Fig. 3a–r), Riul et al. (2013) Freshwater: Poulos et al. (2012a,b)	Occurrence records, environmental layers
Potential distribution of the species along a shipping route	None	ENM workflow, transect plots (this study)	Graph output showing natural versus ship-facilitated spread	This study (Fig. 4), Freshwater: Boets et al. (2013)	PD maps of the species
Potential distribution of the invasive species worldwide	None	ENM workflow (model an invasive species in its native range and project the model in the area of interest), ESW DIFF workflow (this study)	PD map and statistics	This study (example <i>Mytilopsis leucophaeata</i> see discussion)	Global marine layers aquamaps.org oracle.ugent.be occurrence points of the species in the native range corpi.ku.lt/databases/index.php/aquanis or gbif.org/
Detection of invasive species hot spots	Monitoring in ports, literature surveys, invasive species databases	ESW-STACK workflow (this study)	PD map and statistics	This study (Fig. 2)	Multiple invasive species PD maps
Potential impacts of an introduction	Expert opinion	Expert opinion	None	–	–
Potential invasive risk under future climates	None	ENM workflow, ESW DIFF workflow	PD map and statistics	Leidenberger et al. (2015), Jeschke and Strayer (2008)	Occurrence records, climate prediction environmental layers aquamaps.org

4.3. Natural-spread versus ship-facilitated invasions

The comb jelly *Mnemiopsis leidyi* represents one example of possible natural spread. This species shows suitable habitats in the Baltic Proper (Bornholm Basin, salinity around 7 PSU, Table 2, Fig. 3m), but other studies show that it is not able to establish self-sustaining populations there yet (Schaber et al., 2011). *M. leidyi* is most likely re-introduced from the Skagerrak and Kattegat to the Baltic Sea each season through drift (September–February) (Haraldsson et al., 2013). Population genetic studies (Reusch et al., 2010) identified the origins of Baltic populations in New England, USA and suggest a secondary colonization event in the North Sea from the Baltic Sea or an independent gene pool coming directly from the American east coast by ballast water transport. In our study, PD maps predicted a wide distribution in the Baltic Sea as well as in the North Sea for the comb jelly. Kube et al. (2007) observed overwintering of a subpopulation in the Mecklenburg Bay, Germany and Lehtiniemi et al. (2012) recently suggested a suitable habitat for successful reproduction of *Mnemiopsis leidyi* in the southern parts of the Baltic Sea. Even if temperature might actually be at present the limiting factor for this species to establish breeding populations (Table 2), this could change if temperatures rise during the next 80 years by +4 °C as predicted in this area (Meier et al., 2012).

The benthic Chinese mitten crab, *Eriocheir sinensis*, is another classic example of a non-native species becoming invasive. It was

at first observed occasionally in the Baltic Sea (Ojaveer et al., 2007) and its breeding ecology suggested that no self-sustaining populations could be formed in low salinity waters (Anger, 1991). Today, however, the number of observations reported in Baltic waters has increased and an established population has been described (Drotz et al., 2010; Otto and Brandis, 2011). In our study, the PD map for *E. sinensis* shows suitable habitats in nearly the entire Baltic Sea (Fig. 3d). Population genetic analyses have found differentiation in haplotype composition and evolutionary adaptation between the colonized European and original populations (Wang et al., 2009). The potential for natural spread along the European coast is also high for this species, as there are no gaps in the potential distribution area along the entire coast (Fig. 3d). Potential risk of introduction through ballast water exchange is also high as habitat suitability is high throughout almost the entire shipping route analyzed (Fig. 4a).

4.4. Integrating SDMs into non-indigenous species risk assessments

Model-based information can be a useful complement to existing RA models for ballast water exemptions (see Table 4), based on environmental and biogeographic matching (BWMC, 2004; IMO, 2004). It allows us to predict suitable habitats and forecast distribution changes using future climate models (Jones et al., 2013; Leidenberger et al., 2015). Today, important environmental raster data for benthic marine environments are still lacking to further

improve ENM (e.g. substrate data or bottom temperature and salinity layers), but such data may become available in the near future.

The methods presented in this study can provide standardized outputs than could complement conventional RA methods with important predictive information on NIS (Cooper et al., 2012; David et al., 2013a; Liu et al., 2014). However, there are documented limitations to SDM, due to insufficient biological data, spatial bias, temporal bias, lack of absence data as well as lack of environmental layers, poor resolution and collinearity in the data. In addition, the performance of different models varies considerably in terms of model accuracy. Choice of model should be fit for purpose and reliability of the prediction should be assessed using AUC and/or OE (reviewed in Reiss et al., 2014). One possible drawback of using SDM in decision making is that it offers high uncertainty and thus higher risk of misinterpretation of results. Desired information for decision making often consists in a single prediction with little uncertainty (Jones et al., 2013), such as in the risk assessment framework for exemptions for ballast water management (David et al., 2013a). One has to ask if these simple predictions are adequate and if they reflect the complexity of the biological systems analyzed. Jones et al. (2013) discusses the limitations of science in delivering a “true” picture of the ecosystem, rather than a simplified model for decision makers, and proposes multi-model approaches, which could also limit the decision-making process if variability in prediction leads to confusion. SDMs offer a broad possibility of multi-model approaches, e.g. through different algorithms and climate scenarios. Analytical portals, like the one used in this study, may offer a comprehensive approach, where multiple models run using a large number of algorithms (MaxEnt, SVM, EnvDist) and parameters (e.g. layers and scenarios) can be tested for many species (sweep function) at the same time.

In future, SDMs could be produced for multiple species to identify hot and cold spots along major shipping routes. For example, top 50 invasive species could be modelled, assuming species occurrence data are available for those species, especially from their native distribution area.

Current non-indigenous species RAs based on biogeographic matching are very regional and/or are concentrated on a single NIS only (Kotta et al., 2013; David et al., 2013a; Collingridge et al., 2014). Our study shows that SDM based approaches have the potential to include global models in RAs, which is desirable considering that most NIS are translocated by global ship traffic. SDM offers the possibility of global habitat modelling, which could complement traditional environmental matching methods performed on a local scale (Table 4). As there are few physical dispersal barriers for species in fully marine environments, SDM approaches seem to be even better suited to marine than to terrestrial ecosystems (Robinson et al., 2011). In addition, because species' ranges conform closely to their thermal limits in aquatic systems, ENM can yield a more accurate prediction of range shifts than on land (Sunday et al., 2012).

4.5. e-Science approaches in environmental management

ENM offers a comprehensive way to map potential habitat suitability for NIS and helps us understand potential effects on ecosystems before invasions take place. Coupling this approach with the increasing availability of primary biodiversity and environmental data (e.g. from GBIF and Bio-Oracle) can lead to improved RAs. Currently, the major limitation is that many environmental data layers such as sediment type (an important parameter for benthic organisms) are not available on a larger spatial scale. But such data often exist, although in distributed form and in non-standard formats. Here, workflow approaches can be employed to access a wide range of distributed sources and automatically generate harmonized data such as for example large scale and high-resolution

sediment and habitat layers. These layers can then be used for a wide range of biological modelling applications, as for example in our study.

Another critical problem is the taxonomic bias in most biodiversity databases, which typically have a strong over-representation of well-known organisms from well known parts of the world, while data for many potential and actual NIS are not available online. Examples are *Coscinodiscus wailesii* and *Crassostrea gigas* which have plenty of occurrence records in GBIF (gbif.org), while other notorious invaders like *Mnemiopsis leidyi* are ‘off the radar’ in most biodiversity databases (Table 1). Such missing data have to be assembled through scientific networks and manual literature digitization, which are time-consuming processes. Here, analytical platforms allow collaboration and faster aggregation of relevant data and knowledge to predict global marine invasion patterns.

Automated data mining and database querying methods, like the *Taxonomic Data Refinement* workflow are important steps towards accessing and integrating large amounts of biodiversity data from a wide range of sources. For example, literature digitized by the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org>) will eventually become machine-searchable and can be accessed through the workflow in the future to find relevant data and feed these into ENM. Also, an open source, frequently updated world database of occurrence data for NIS, where scientists as well as authorities share datasets on NIS, would be highly valuable for this purpose. One early example is the AquaNIS information system on aquatic non-indigenous and cryptogenic species (<http://www.corpi.ku.lt/databases/index.php/aquanis>).

Another example is the Global Invasive Species Database <http://www.issg.org/database/welcome/> maintained by the IUCN Species Survival Commission.

In our study, the lack of data for the dreissenid bivalve *Mytilopsis leucophaeta* in the area of interest resulted in a weak potential distribution (AUC: 0.967, OE: 6.43%) (Fig. 3g). The actual distribution of this species is likely to be much larger in Europe (Laine et al., 2006; Kennedy, 2011). The same applies for many zooplanktonic or phytoplanktonic species that had to be excluded from the analysis because of a lack of distribution data. Data availability is one of the biggest challenges for effective RAs on non-indigenous species, resulting in a strong demand to improve the contents and connectivity of global and local databases.

4.6. Evolutionary adaptation, climate change, and reintroductions

Species that were thought not to be able to enter the Baltic Sea in the past are well established today (e.g. Alheit et al., 2012). Two important factors that could determine if NIS will become invasive and that might have been underestimated in the past are the adaptive potential of the species as well as the on-going ballast water exchange, functioning as a permanent source of new individuals to replenish the gene pool. Both these factors contribute to the potential to acclimatize to new environments and establish a breeding population (see described examples of *Eriocheir sinensis* and *Mnemiopsis leidyi* above).

A further challenge for non-indigenous species RAs is climate change. For Northern Europe, but especially for the semi-enclosed Baltic Sea, predicted temperature will rise by up to 4°C and salinity is expected to decrease in the Baltic Proper by 1.5–2 PSU through an increase in run-offs during the next 80 years (Meier et al., 2012). These climate changes can lead to higher habitat suitability in the Baltic area for most of the analyzed species, especially those that have origins in warmer regions and a broad salinity tolerance (brackish and freshwater species) (Table 1). Species like *Gammarus tigrinus*, *Rhithropanopeus harrisi* and *Marenzelleria viridis*, for instance, might become more abundant in the Baltic due to an increase in the suitability of abiotic conditions, in contrast to native

Baltic species, which will become more stressed in these new conditions. Today, these NIS are described as strong candidates that are able to outcompete the native species and have strong potential to cause severe consequences in benthic ecosystems (Thomsen et al., 2009; Kotta and Ojaveer, 2012; Kotta et al., 2013).

Due to climate change, new and shorter shipping routes are already being used across the Arctic sea (e.g. the northern sea route or Northwest Passage). The Arctic Geographical Information System offers a web-interface to map shipping routes across the arctic and calculate expected future routes based on different climate models (www.arkgis.org). The use of shipping routes across the arctic is expected to increase in the mid-21st-century as a consequence of global climate change, and might result in higher survival rates for organisms in ballast water as well as fouling organisms (Smith and Stephenson, 2013; Stephenson et al., 2013; Miller and Ruiz, 2014). Such changes will influence the establishment of new NIS, resulting in unpredictable consequences on local benthic ecosystems such as biodiversity loss and homogenization.

5. Conclusions

SDM-based tools presented in this study can contribute to a new generation of RAs (Table 4), where both model and data based decision processes are taken into account. With the exception of ships on certain routes, it will be forbidden to discharge untreated ballast water when the BWM Convention comes into force for all ships, at latest by 2019. Ships can apply for an exemption from ballast water management only on the basis of an RA. This RA should not be based on a single environmental parameter (e.g. salinity) to distinguish between unacceptable 'high' and acceptable 'low' risk scenarios for the shipping route. Future RAs should ideally combine habitat suitability matching by ENM with a species-specific approach. ENMs have the benefit of: (i) taking more environmental parameters into account; (ii) producing PD maps for a single species and measuring their potential habitat suitability in the invaded area; (iii) allowing comparisons between species groups; (iv) calculating accumulated effects of a large number of species; and (v) helping to assess whether a species is able to reach the recipient port through natural spread (Table 4).

We can learn from past experiences, as in the case of *Eriocheir sinensis*, that natural spread of NIS is not limited by salinity tolerance only, but is instead based on a multifactorial description of the species niche. New generations of RAs should take into account all relevant and available sources of information on a NIS to determine its potential for dispersal and establishment. While open-source SDM tools already exist, they need to become more user-friendly and usable in a policy context. A challenging task ahead will be the sharing of global data on NIS that are needed to produce rapid assessments and improve the prevention and management of marine invasions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2015.04.033>.

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