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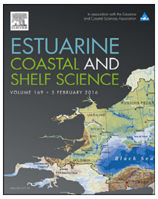

Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby *Neogobius melanostomus* in a regional sea

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ABSTRACT

Introductions of non-indigenous species (NIS) are considered a major threat to aquatic ecosystems worldwide. While it is valuable to know the distributions and ranges of NIS, predictive spatial models along different environmental gradients are more useful for management of these species. In this study we modelled how external drivers and local environmental conditions contribute to the spatial distribution of an invasive species using the distribution of the round goby *Neogobius melanostomus* in the Baltic Sea as an example. Using the collected distribution data, an updated map on the species distribution and its invasion progress in the Baltic Sea was produced. The current range of the round goby observations is extensive, covering all major sub-basins of the Baltic Sea. The most recent observations appeared in the northern regions (Northern Baltic Proper, the Gulf of Bothnia and the Gulf of Finland) and on the eastern and western coasts of southern Sweden. Modelling results show that the distribution of the round goby is primarily related to local abiotic hydrological conditions (wave exposure). Furthermore, the probability of round goby occurrence was very high in areas in close proximity to large cargo ports. This links patterns of the round goby distribution in the Baltic Sea to shipping traffic and suggests that human factors together with natural environmental conditions are responsible for the spread of NIS at a regional sea scale.

1. Introduction

Humans have greatly accelerated the pace of interregional migration of species globally. In aquatic environments, this occurs mainly by transporting species in ballast water, on the hulls of ships, or by releasing exotic aquarium species (Carlton and Geller, 1993). When species are released into new environments their establishment success is affected by the intensity of the propagule pressure for a given species (*e.g.*, Lockwood et al., 2009; Simberloff, 2009; Wonham et al., 2013) and suitability of the habitat in relation to the species' physiological tolerances (Lynch and Gabriel, 1987). This explains why coastal areas of enclosed seas and estuaries, characterized by intense transoceanic shipping and the presence of a wide range of environmental conditions, are some of the most highly invaded environments in the world (Carlton and Geller, 1993).

Accumulating evidence on successful invasion events, as well as, failures of eradication of non-indigenous species (NIS) from the invaded ecosystems, highlight the need for predictive tools for evaluating the risks of invasions at specific locations. The relationship between the number of organisms initially released into the environment and the risk of a successful invasion is theoretically understood (Drake, 2004; Courchamp et al., 2008). However, these models often fail to predict species distributions (*e.g.*, Taylor and Hastings, 2005). In the real world, species invasions often stem from large-scale and repeated releases (Wonham, 2008). These processes are potentially characterized by vector-scale models, which also match the scale at which many preventive regulations are being developed (IMO, 2004; Albert et al., 2013; Lee et al., 2013).

Practical challenges in measuring the propagule pressure

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associated with an invasion vector exist and proxy variables are widely used in analyses to overcome such difficulties (Lockwood et al., 2009; Simberloff, 2009; Haydar and Wolff, 2011). The expected shape of the risk—release relationship is not clear, and both linear and nonlinear models have been applied to empirical data (Ricciardi, 2006; Reusser et al., 2013). Because of this variability, machine learning techniques are a useful method to empirically determine the shape and strength of risk-release relationships, as they do not limit the outcome to pre-determined data models but rather use an algorithm to learn the relationship between the response and its predictors Thereby, machine learning techniques can fit a diverse array of functional response curves (Hastie et al., 2009).

The round goby, *Neogobius melanostomus* (Pallas 1814), is a successful and widespread invader worldwide and is considered one of the most invasive NIS in the Baltic Sea (Kornis et al., 2012). It was first observed in the Baltic Sea in Poland in 1991 (Skóra and Stolarski, 1993) and later recorded in several other areas of the Baltic Sea (AquaNIS, 2014). Round goby is a territorial, aggressive, and voracious generalist benthivore reported to prefer bivalves when they are available (Marsden et al., 1997; Kornis et al., 2012). As shipping is likely behind the invasion of the round goby (Sapota and Skóra, 2005; Kornis et al., 2012), useful proxies for propagule pressure include: distance to harbour, historic records of vessel traffic, tonnage and ballast volume of ships. These proxies are easy to define and therefore have been widely used in earlier bioinvasion studies (Jazdzewski et al., 2005; Ricciardi, 2006; Lo et al., 2012; Chan et al., 2013).

Apart from propagule pressure, extensive knowledge on environmental tolerances of the species is needed in order to model their distribution in the invaded ecosystem. Even though a region may have a high probability for invasion, local biotic and abiotic characteristics determine the success of establishment and reproduction (Lynch and Gabriel, 1987; Roura-Pascual et al., 2011). Assessing environmental factors related to the presence of the round goby therefore requires knowledge of the prevailing physical and chemical conditions in the invaded locations. Once these optimal conditions are empirically documented, the relationships can be used to predict the probability of the presence of the round goby along measured environmental gradients. Although considered one of the most invasive NIS in the Baltic Sea and worldwide, development of a spatial predictive model for the round goby had previously been hampered by a lack of information about its current distribution and environmental preferences in the invaded ecosystems (Shearer and Grodowitz, 2010; Ojaveer and Kotta, 2014).

In contrast to many native species, successful NIS often tolerate broad ranges of environmental conditions and can even adapt life history strategies to local conditions in the invaded environments (*e.g.*, reproduction, see Platt and Jeschke, 2014). Anthropogenic transfer processes infer a bottleneck on NIS, which assures that only the hardiest individuals arrive to the new location. Therefore, surviving individuals will theoretically be better suited for establishment and further expansion (*sensu* Blackburn et al., 2011). Similarly, the round goby has shown great establishment success in several invaded ecosystems due to favourable environments and several species-specific traits (Charlebois et al., 2001). The secondary spread of NIS within a new ecosystem may occur through a combination of natural dispersal and anthropogenic transport mechanisms (Minchin et al., 2009). When water bodies are interconnected, secondary dispersal of NIS may effectively take place as active migration and/or movement by water currents (*e.g.*, Minchin et al., 2009). Human-induced dispersal mechanisms can also contribute to their secondary spread. The larvae and early juveniles of the round goby, similar to several demersal fish species, undergo diel vertical migration and therefore nocturnal ballasting can result in the transport of larval and young round gobies (Hensler and Jude, 2007; Hayden and Miner, 2009). Moreover, the gobiidae are known to lay eggs on hulls or within sea-chests (Wonham et al., 2000; Jude et al., 1995) and their pelvic fins reduce maintenance costs while carried within ships' ballast water (French and Jude, 2001). Such a combination of characteristics may explain why this group of fishes have been generally more successful over other fishes by shipping transport. However, distribution and spread of NIS may not be fully predictable as each invasion has a strong stochastic element. Moreover, if the establishment process of NIS is still in progress, *i.e.*, the species has not yet filled all of their potential niche space, then relationships between the environment and species distribution pattern may not emerge.

In the current study we modelled how external drivers and local environmental conditions relate to the probability of occurrence of the round goby. We analysed whether areas where the round goby has been observed in the Baltic Sea share certain specific abiotic characters or whether the current distribution of the round goby is largely uncoupled from its abiotic environment and is primarily defined by the intensity of propagule pressure *i.e.* shipping. We expect that large-scale environmental stresses and disturbances, such as climatically driven changes in seawater temperature or wave exposure, can synchronize population changes over wide geographical areas, as they have a potential to affect recruitment or mortality of the round goby and its prey. Nevertheless, as the round goby is territorial with limited swimming range (Ray and Corkum, 2001), we also expect that shipping intensity increases the probability of occurrence of the species. We also aim to show how and to what degree the distribution pattern of the round goby is explained by eutrophication. We expect that eutrophication, one of the key disturbances in the Baltic Sea, plays an important role in dispersal of the round goby by increasing nutrient loads and, therefore, promoting higher invertebrate abundances including the most preferred food items of the round goby (Kotta et al., 2009; Järv et al., 2011), ultimately resulting in an increase in the probability of occurrence of the fish. Although, the roles of facilitation and inhibition by resident fauna are dominant themes in the invasion literature (*e.g.*, Elton, 2000; Gurevitch et al., 2011), apart from eutrophication-induced effects of the prey, we focused our scope to propagule pressure and abiotic drivers. This is because the round goby has been ranked among the most aggressive demersal fishes in the Baltic Sea range and competition and predation by native fish species only marginally impact the gobies' densities and their spread (Marsden et al., 1997; Järv et al., 2011).

2. Material and methods

2.1. *The study area*

The Baltic Sea is an example of an environment where biological invasions are becoming increasingly widespread, posing a serious threat to biodiversity and ecosystem (Olenin et al., 2007; Zaiko et al., 2011; Ojaveer and Kotta, 2014). As a typical representative of a temperate semi-enclosed brackish sea, it has extensive coastal areas characterized by basin-scale gradients of temperature, salinity, and oxygen content (Segerstråle, 1957). Ever-increasing maritime shipping and other invasion vectors maintain the elevated propagule pressure of non-indigenous species into the Baltic Sea (HELCOM, 2010). On top of this, a majority of the projected climate change scenarios suggest extreme shifts in the Baltic Sea environment (BACC, 2008), which will further destabilize local environment and create space for novel non-indigenous species. These conditions, together with spatially variable and relatively low overall species richness (Ojaveer et al., 2010), broadly define the ‘invasion environment’ of the Baltic Sea favourable for both new arrivals as well as secondary spread of already existing non-indigenous species (NIS).

2.2. Round goby distribution data

As only one country has marine alien species monitoring program in place in the Baltic Sea (ICES, 2012), the knowledge of the current distribution range of the round goby is scattered and incomplete. In the current study all the existing information on the round goby in the Baltic Sea basin was systematically reviewed and recorded as “presence” along with the observation year (from 1990 to 2014) and formatted into a geo-referenced distribution dataset. Data for round goby observations were obtained from various sources: literature (*e.g.* annual reports of the Working Group on Introductions and Transfers of Marine Organisms of the International Council for the Exploration of the Sea (ICES WGITMO); Wandzel, 2000; Bacevičius, 2003; Corkum et al., 2004; Sapota, 2004; Ojaveer, 2006; Rakauskas et al., 2008; Kornis et al., 2012; Rakauskas et al., 2013; Azour et al., 2015); public web pages presenting round goby observations (ArtDatabanken, 2014; Finnish Alien Species Database, 2014; Fischfauna-Online, 2015); authors own data, originating both from coastal fish monitoring programs as well as contacts with local professional and recreational fishermen (mainly from Estonia, Lithuania and Latvia).

Since coastal fish monitoring efforts and methods vary between locations, estimating round goby abundances was impossible. Nevertheless, the gobies' observations covered broad ranges of environmental gradients and spanned vast areas across the geographic space (*e.g.*, port and remote areas). A comparison of the distribution of goby locations to the distribution of background locations in environmental space showed that these statistical distributions were similar; thus, sampling bias was not a concern.

Maps presenting round goby invasion in the Baltic Sea were created using QGIS software (Quantum GIS Development Team, 2014). All round goby observations ($n = 333$) where used in the distribution map and in the MaxEnt model (see the modelling chapter below).

2.3. Supporting environmental data

The round gobies' distribution dataset was supplemented with the key environmental data potentially impacting the establishment and spread of this invasive fish species (Table 1). All environmental variables were continuous. Investigated variables included the following proxies of propagule pressure: shipping intensity (Density of ships equipped with Automatic Identification System, monthly average per pixel of 2200 × 2200 m size; HELCOM, 2014), amount of annual cargo traffic at a nearest port (tons; HELCOM, 2014) and distance to nearest port (km). Variables characterizing the tolerance of round goby to abiotic environment included vertically aggregated mean seawater temperature (°C), maximum salinity (psu), stratification (mean difference in water density between surface and bottom layers i.e. mixing intensity, kg m^{-3}), exposure to waves ($m^2\ s^{-1}$) and depth (m). As a proxy for eutrophication the surface water, chlorophyll *a* (chl *a*, mg m^{-3}) and water attenuation coefficient (K_d) were used.

Shipping intensity data were obtained from the HELCOM data service. The raw AIS data were averaged over months and then the resulting layer was converted into a raster image. Similarly, information on ports and associated cargos was extracted from the HELCOM portal at http://maps.helcom.fi/website/mapservice/index.html.

The values of water temperature, salinity and stratification were obtained from the hydrodynamical model calculations from April to August 2005–2012. The calculations were based on the COHERENS model, which is a primitive equation ocean circulation model. It was formulated with spherical coordinates on a 10 × 10 min horizontal grid and 30 vertical sigma layers. The model was forced with hourly meteorological fields of 2 m air temperature, wind speed, wind stress vector, cloud cover and relative humidity. The meteorological fields were obtained from an operational atmospheric model. The model was validated against water level, temperature, salinity and water velocity measurements from the study area (Bendtsen et al., 2009).

The Simplified Wave Model method was used to calculate the wave exposure for mean wind conditions represented by the ten year period between 1 January 1997 and 31 December 2006 (Isaeus, 2004). A nested-grids technique was used to take into account long distance effects on the local wave exposure regime. The resulting grids had a resolution of 25 m. In the modelling the shoreline was divided into suitable calculation areas and fetch and wave exposure grids were calculated. Subsequently the separate grids were integrated into a seamless description of wave exposure along the study area. This method results in a pattern where the fetch values are smoothed out to the sides, and around island and skerries in a similar way that refraction and diffraction make waves deflect around islands. The depth raster was obtained from the database of the Estonian Marine Institute (version 2014).

As a proxy for eutrophication the MERIS satellite derived water transparency (K_d) and water chlorophyll *a* (chl *a*) values were used. The frequency of satellite observations was generally every second day over the whole ice-free period (years 2009–2014). However, several observations were discarded due to cloudiness. The spatial resolution of satellite data was 300 m. False zeroes, for example resulting from cloudiness, were removed from the data prior to the statistical analysis.

2.4. Modelling

In locations where species data have been collected systematically, for example through biological monitoring, both presence

Table 1
Environmental variables used in the MaxEnt models.

No	Variable	Unit	Function in model	Type of data	Years of collection	Spatial resolution
1	Shipping intensity	coefficient	Propagule pressure	Continuous	2014	2200 m
2	Cargo traffic	tons	Propagule pressure	Continuous	2014	Not relevant
3	Distance to port	km	Propagule pressure	Continuous	2014	Not relevant
4	Mean temperature	°C	Abiotic environment	Continuous	2005–2012	1000 m
5	Maximum salinity	psu	Abiotic environment	Continuous	2005–2013	1000 m
6	Mixing intensity	kg m^{-3}	Abiotic environment	Continuous	2005–2014	1000 m
7	Exposure to waves	$m^2\ s^{-1}$	Abiotic environment	Continuous	1997–2006	25 m
8	Depth	m	Abiotic environment	Continuous	2014	50 m
9	Chlorophyll *a*	mg m^{-3}	Eutrophication	Continuous	2009–2014	300 m
10	K_d	coefficient	Eutrophication	Continuous	2009–2014	300 m

and absence of species at each site have been recorded. However, in most locations round goby observations were collected non-systematically and available as presence-only records and traditional modelling tools could not be used. In order to maximize the utility of the database, presence-only species distribution modelling was used instead.

In this study the contribution of each environmental variable on the probability of occurrence of round goby in the Baltic Sea range was explored using the MaxEnt method. MaxEnt is a machine learning algorithm for modelling species distributions from presence-only species records. In brief, MaxEnt seeks what makes the environment of the occurrence localities of a species different from the environment in the whole geographical region of interest. Based on the observed mismatch a species' distribution is defined. More specifically, MaxEnt model minimizes the relative entropy between two probability densities (one estimated from the presence data and one, from the landscape) defined in covariate space. When doing so the model compares the density of covariates in the region to the density of covariates occupied by the species and such comparison informs us what environmental variables are important and estimates the relative suitability of one location vs. another. The null model for the raw distribution is uniform distribution over the landscape, since without any data we would have no reason to think the species would prefer any location to another. MaxEnt's predictive performance is consistently competitive with the highest performing methods. Since becoming available in 2004, it has been utilized extensively for finding correlates of species occurrences, mapping current distributions, and predicting to new times and places across many ecological, evolutionary, conservation and biosecurity applications (Elith et al., 2006).

Multicollinearity can be an issue with MaxEnt when answering if and when environmental variables are of ecological interest. Thus, prior to modelling, a correlation analysis was conducted for environmental variables and the final MaxEnt models included variables that were not significantly correlated with each other (at $p < 0.05$). Among the studied environmental variables only the proxies of propagule pressure correlated (between shipping intensity and distance to nearest harbour $r = -0.29$; $p < 0.001$). Thus, in order to avoid multicollinearity issue and to assess their usefulness in predicting the distribution of round goby, separate models were run for each of the shipping proxies.

In this study MaxEnt models were fitted as combinations of basic functions and features. MaxEnt had six feature classes: linear, product, quadratic, hinge, threshold and categorical. Products were all possible pairwise combinations of covariates, allowing simple interactions to be fitted. Threshold features allowed a “step” in the fitted function; hinge features were similar except they allowed a change in gradient of the response. Many threshold or hinge features were fitted for one covariate, giving a potentially complex function.

Segment-based (non-gridded) data were modelled using SWD (samples-with-data) format in MaxEnt for both presence and background sites (*i.e.*, the whole Baltic Sea). A 10-fold cross-validation was used to obtain out-of-sample estimates of predictive performance and estimates of uncertainty around fitted functions. In order to reduce model overfitting, a balance between accurate prediction (model fit) and generality (model complexity) was sought by maximizing the penalized maximum likelihood function, *i.e.,* the gain function. When doing so, regularization or the LASSO penalty was applied by exploring a range of regularization parameter values and choosing a value that maximizes measures of fit on a cross-validation data set. The LASSO penalty is based on the rationale that features with larger variance should incur a larger penalty and, thus be less likely to be included in the model (Hastie et al., 2009). For model validation a random selection of 25% of the overall localities of round gobies were used. The percent contributions of individual variables to the final model were identified with jackknife tests. The jackknife test evaluates how each variable contributes to the “gain” of the MaxEnt's model (*i.e.*, improvement in penalized average log likelihood compared to null model) (Elith et al., 2011). A variety of error measures can be calculated when comparing modelled and observational data. In particular, the use of threshold-independent receiver operating characteristic (ROC) plots has received considerable attention. A ROC plot is obtained by plotting all true positive fraction (i.e. correctly classified values) on the y-axis against their equivalent false positive fraction for all available thresholds on the x-axis. The area under the ROC function (AUC) is usually taken to be an important index because it provides a single measure of overall accuracy that is not dependent upon a particular threshold. The value of the AUC is between 0.5 and 1.0 with $\text{AUC} = 1.0$ indicating that the model has a perfect match and $\text{AUC} = 0.5$ indicating that model is no better than random (Fielding and Bell, 1997).

3. Results

The current range of round goby observations in the Baltic Sea is extensive (Fig. 1). Since the first observation in 1990, the species has been detected in all major sub-basins. It appears that during the first decade of invasion, the distribution area was mostly confined to the Gulf of Gdansk area, while further spread to the south-western Baltic was observed during the first half of the 2000s. The most recent observations appear in the northern regions (Northern Baltic Proper, the Gulf of Bothnia and the Gulf of Finland) and on the eastern and western coasts of southern Sweden. Currently the northernmost observations are from Bothnian Bay (Raahe, Finland in 2012).

MaxEnt models explained a majority of the round goby distribution, inferring that selected variables were largely responsible for observed pattern in species presence. The cross-validated AUC for the model was estimated at 0.978 indicating that the model has almost a perfect match. However, the AUC plot for MaxEnt involves the fraction of the total study area predicted present instead of the more standard omission rate, *i.e.*, the fraction of absences predicted present. Thus, the presented AUC value is not directly comparable to a standard ROC/AUC approaches involving specificity and sensitivity.

The model suggested that both local hydrography and propagule pressure (measured as shipping activity) largely determine the distribution of the round goby in the Baltic Sea. It appeared that the round goby has an affinity towards locations characterized by low exposure to waves, low salinity, high temperature and high vertical mixing of the water column. In addition, reduced distance to a nearest port and elevated amount of cargo traffic at the port increased the probability of the round goby occurring at a location (Figs. 2 and 3). Although all proxies of propagule pressure contributed to the MaxEnt models, distance to nearest port had the highest predictive power (Table 2). When cargo traffic or shipping intensity was used as a proxy for propagule pressure, exposure to waves was even more important in the MaxEnt models.

Jackknife test showed that exposure to waves contributed over 60% of the model variability *i.e.*, this variable contained information to the largest extent that was not present in other variables. Distance to a nearest port explained 17.6% of model variability, whereas other variables contributed only marginally to the model. Interestingly, eutrophication-related variables such as water chlorophyll *a* level and water transparency as well as water depth did not significantly change the probability of occurrence of the round goby and had only minimal impacts to the final model (contribution below 1.4%). Removal of exposure to waves significantly

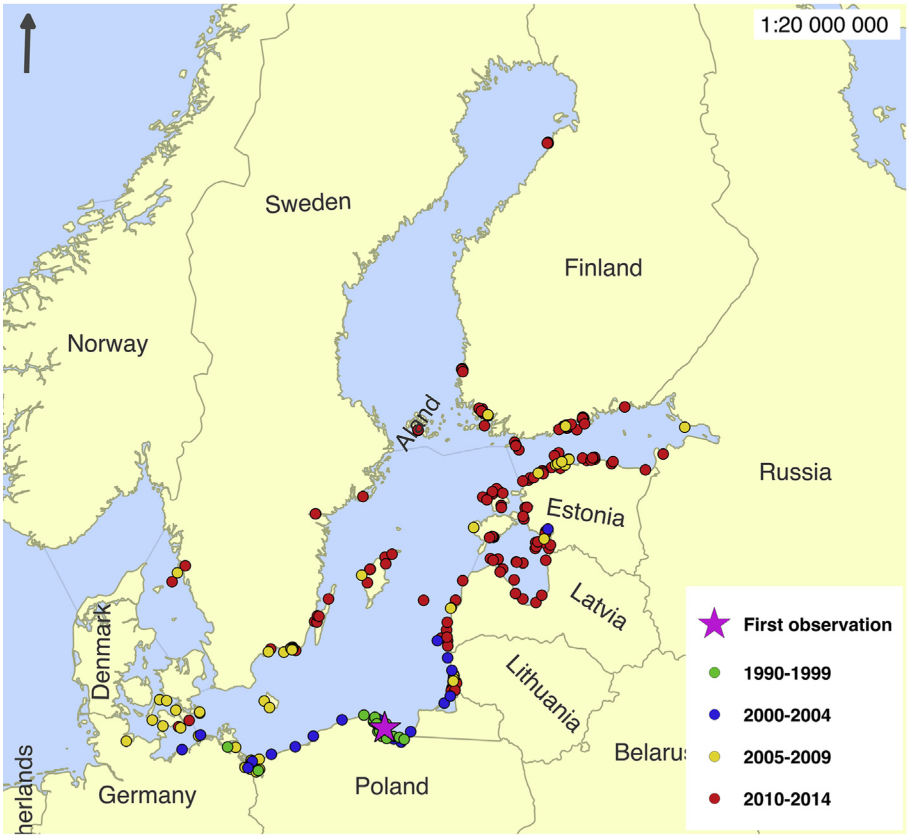

Fig. 1. Observations of the round goby in the Baltic Sea.

reduced the overall predictive performance of models and increased the contribution of depth in the MaxEnt models (Table 2), demonstrating that coastal topography and wave climate play a major role in driving the current distribution of the round goby.

4. Discussion

Since the range of an invasive species is an important predictor of their large scale impacts (Parker et al., 1999) and the best predictor of range size is time after invasion (Byers et al., 2015), one of the most urgent challenges in bioinvasion science is to accurately predict distribution and potential spread of NIS in order to inform stakeholders on invasion risks and suggest management actions. However, as each invasion has a strong stochastic element and NIS may spread far beyond their native niches (Parravicini et al., 2015), development of such predictive models is still hampered by our limited knowledge on the relative contribution of mechanisms behind each bioinvasion, and the roles of the environment modulating species establishment and their further spread (Roura-Pascual et al., 2011). When NIS has already established in the recipient ecosystem, we can learn greatly from the species–environment relationships and estimate to what extent the invasion success is related to the intensity of propagule pressure and/or species tolerance to specific set of local abiotic characters.

The MaxEnt models used in this study performed very well (AUC between 0.978 and 0.980) indicating a significant role of the selected environmental variables to the spatial distribution of the round goby. As the environmental proxies were carefully selected from the literature, the final models describe the best physiological requirements, potential niche space and ecology of the species. Importantly, the model demonstrated that only a handful of environmental drivers are needed to accurately predict the occurrences of the round goby. This suggests that there are very few factors influencing the round goby dispersal in the Baltic Sea.

Among natural drivers, exposure to waves was by far the most important variable defining the environmental envelope of the round goby, low exposure sites being characterized by higher probability of occurrence of the species. This result suggests an affinity of the round goby to sheltered and moderately exposed areas. Round goby is an extremely sedentary species (Ray and Corkum, 2001) and highly exposed areas with a narrow macroalgal belt lacking habitat stability, provide only a limited amount of suitable habitat for the species. In such habitats food is not limiting, as exposed reefs of the Baltic Sea are often covered by a dense population of bivalves (Kotta et al., 2013) indicating a tradeoff between suitable habitat and availability of preferred prey.

As aquatic pollution may increase the relative success of invasive species (Crooks et al., 2010) and, specifically, the round goby has been found to be tolerant to contamination (McCallum et al., 2014), our results indicate that preference of coastal areas by the species might be simply related to the fact that coastal areas are under higher anthropogenic impact than offshore areas. Also, it should be mentioned that our data mostly originate from fishers in the period of spawning and feeding time, when the species is present in the coastal areas. In the cold season, the fish has also been observed in deep offshore areas both in its native and invaded areas (Kostyuchenko, 1969; Walsh et al., 2007). The observed exposure–occurrence relationship may also apply elsewhere, as to date the round goby has also failed to establish in the exposed areas of the Great Lakes (Grigorovich et al., 2003b; Daniel Heath, Personal Communication).

In the current study, the probability of round goby occurrence

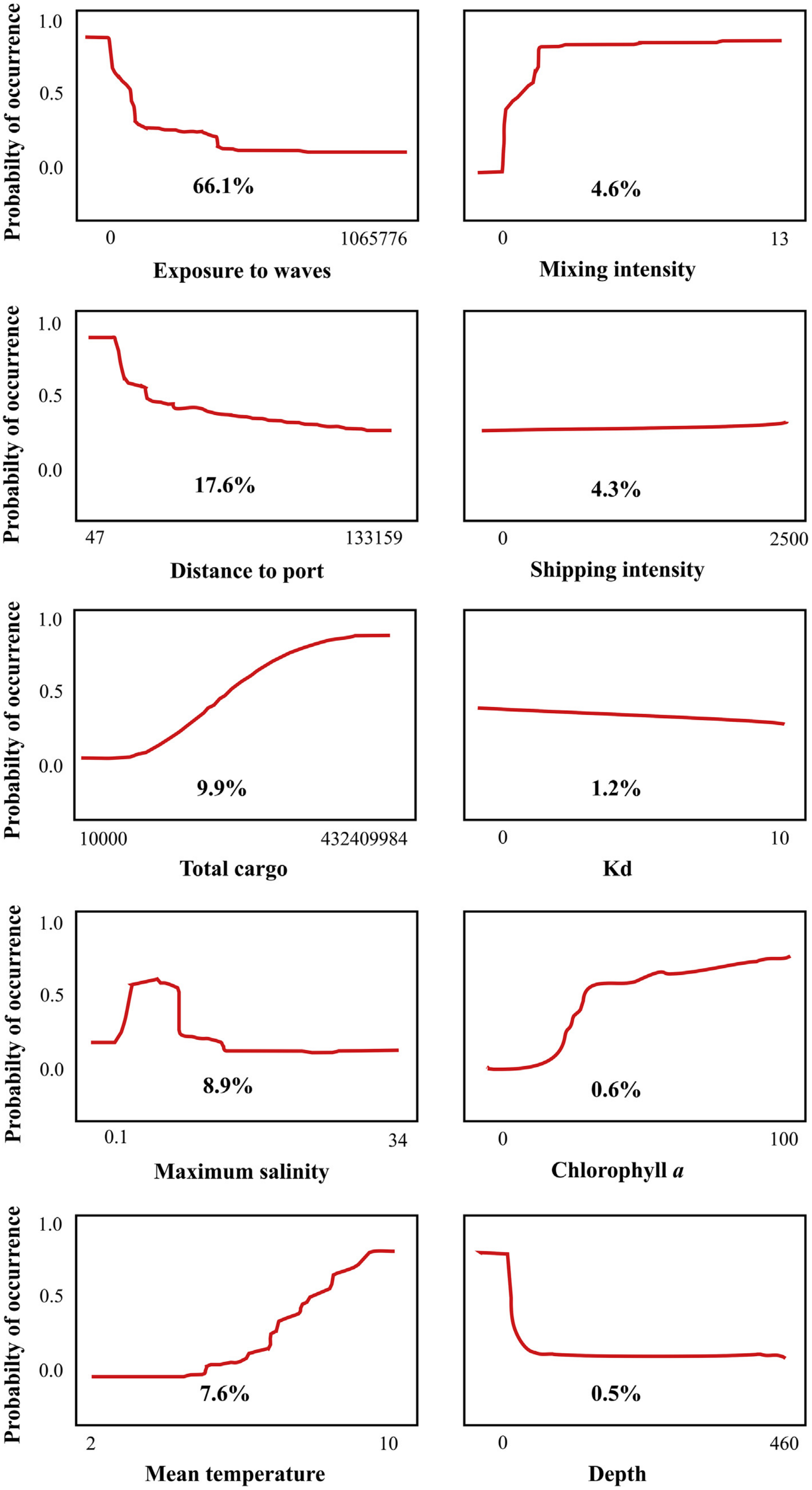

Fig. 2. Dependence plots showing how each environmental variable separately affects the MaxEnt prediction i.e. each of the following curves represents a different model using only the corresponding variable. The separate contribution of each variable is shown in each graph (%). The y-axes indicate logistic output.

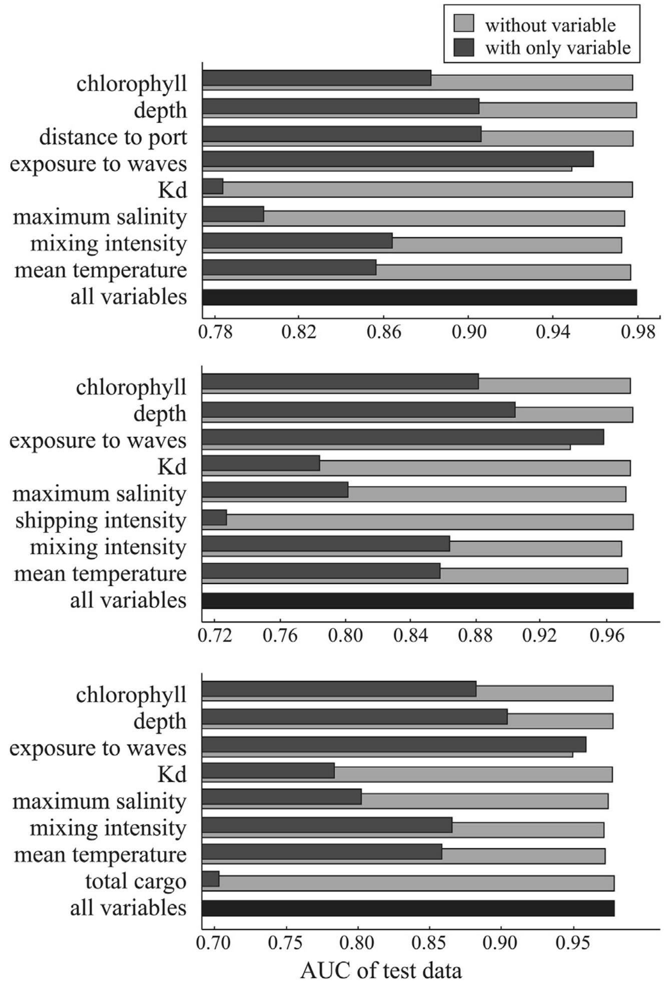

Fig. 3. Results of the jackknife test of variable importance in the MaxEnt models. In these tests test gain was used. In this analysis the environmental variable that decreases the gain the most when it is omitted has the most information that is not present in the other variables.

Table 2
Results of MaxEnt models run separately for each three shipping proxies: distance to port, total cargo and shipping intensity. Separate models were run to avoid multicollinearity issue in the MaxEnt models as shipping intensity and distance to nearest harbour were weakly intercorrelated ($r = -0.29$; $p < 0.001$). Models' descriptive power and percent contributions of each variable to the relevant MaxEnt models are shown. The AUC is a measure of overall model accuracy with the values above 0.9 suggesting almost a perfect match of all three models. Unregulized test gain is a measure of goodness of fit of models. It represents the presence likelihood of training records in comparison with background records. Gain is not regularized/compensated for the number of terms in the model.

Model descriptive power/variable	1	2	3
Test data AUC	0.980	0.978	0.978
Unregulized test gain	3.525	3.513	3.511
Distance to port	17.6		
Total cargo		9.9	
Shipping intensity			4.3
Exposure to waves	61.9	67.7	68.8
Salinity maximum	8.4	8.4	10
Temperature mean	6.1	7.8	8.8
Mixing intensity	4.1	4.3	5.5
Depth	0.4	0.6	0.6
K_d	1.3	0.8	1.4
Chlorophyll *a*	0.3	0.6	0.8

was significantly higher in close proximity to ports characterized by elevated cargo amounts. This clearly links patterns of the round goby distribution to the cargo traffic and is in line with evidence from elsewhere suggesting that the human factor (national wealth and human population density) is a significant predictor in the majority of models when analysed jointly with climate, geography and land cover (Pyšek et al., 2010). When cargo tonnage or shipping intensity was used as a proxy for propagule pressure, exposure to waves gained importance in the MaxEnt models. This may indicate that proximity to ports was the best proxy for describing propagule pressure.

The North American Great Lakes also host very dense populations of the round goby. Since its apparent arrival via ballast water in 1990 (Jude et al., 1992) the species is widely distributed across all of the five lakes and is spreading rapidly into adjacent tributaries (Jude, 2001; Kornis and Vander Zanden, 2010). Substantial genetic variation, multiple founding sources, large numbers of propagules, and a unique population structure is likely behind this ecological success story (Brown and Stepien, 2009).

Recent genetic analyses demonstrated that a combination of short-distance diffusion and long-distance dispersal contributes to the current distribution of the round goby in the lakes and rivers of its introduced North American ranges (Bronnenhuber et al., 2011). This evidence also suggests that commercial shipping potentially promotes frequent long distance spread of the round goby in these habitats (LaRue et al., 2011). Although different in methodologies, the North American studies and our paper have independently come to a similar conclusion, and jointly suggest that the spread of the round goby can largely benefit from shipping.

There are several examples outside of the Baltic Sea to suggest that shipping is a likely pathway for the invasion of gobies. In their review, Wonham et al. (2000) concluded that gobies (family Gobiidae) were the most commonly found fish in ballast tanks and they also dominate among fishes introduced via ballast water. There are several reasons why gobies have been more successful over other fishes by shipping transport. Specifically, gobies are known to be resilient enough to survive ocean crossings in ballast tanks (*e.g.*, Carlton, 1985, 1987) owing to the existence of a specialised lateral-line system (Jude, 1997) and tolerance of a wide range of habitat conditions (Kornis et al., 2012). The crevicolous nature of gobies when seeking refuge and laying eggs may predispose them to ballast-water transport, particularly due to the ballast-intake grates (Hoese, 1973; Carlton, 1985). Gobies may also lay eggs in small holes and thereby use ship hulls as a transport vector (Wonham et al., 2000). The recent cases of ships' ballast water transfers (as larvae or juveniles) include the introduction of the Australian bridled goby, *Arenigobius bifrenatus* to New Zealand (Willis et al., 1999) and the streaked goby *Acentrogobius pflaumii* into southwestern Australia (Maddern and Morrison, 2009).

Earlier theoretical models have shown that relationship between species release and establishment can potentially have only two shapes: hyperbolic or sigmoid (Wonham, 2008). MaxEnt models in this study demonstrated a sigmoid curve between the amount of cargo and the probability of occurrence of the round goby. This implies a clear Allee effect, *i.e.*, invading goby individuals interact positively creating an accelerating phase of a sigmoid curve (Allee, 1931). Previous studies have demonstrated either absence or presence of risk–release relationships (*e.g.*, Grigorovich et al., 2003a; Ricciardi, 2006; Costello et al., 2007). Such discrepancies may simply suggest that for some ecosystems or species, post-release processes have an overwhelming role over propagule pressure, whereas, for other ecosystems or species, propagule pressure is primarily limiting the spread of non-indigenous species. Alternatively, the selected proxies of propagule pressure may mismatch the measured species occurrences in space, time, or taxonomic resolution (Wonham, 2008). However, the MaxEnt models in this study suggested that both distance to ports and net mass of cargo are good proxies of propagule supply of the round goby and therefore can be used in a scientifically based management tools also when modelling other shipping related NIS distributions.

Temperature and salinity regime contributed only marginally to the model variance implying that the round goby has low sensitivity to environmental extremes, potentially due to either large variation in between-individual environmental optima and/or broad within-individual plasticity (Roughgarden, 1972; Abedikova, 1980; Kornis et al., 2013). Similarly, elevated chlorophyll *a* level, used as a proxy of eutrophication measure, did not yield to higher probability of occurrence of the round goby. It is likely that at the initial stage of invasion, food is not limiting the spread of this invasive fish. In general, clams and mussels constitute the majority of benthic biomass in the coastal areas of the Baltic Sea and due to a very low natural richness of epibenthic predators this food source is in excess for novel invasive species, such as the round goby (Kotta et al., 2008). Moreover, the diet of round gobies is not limited to bivalve prey. In areas where bivalves are less abundant, gobies easily consume other available prey species such as barnacles, gastropods, and chironomids (Riikka Puntila, Unpublished Data). Similar results have been observed in other areas for similar species, such as the shimofuri goby *Tridentiger bifasciatus*, who appeared to be a generalist predator in the invaded San Francisco Estuary by consuming seasonally most abundant benthic invertebrate prey (Matern and Brown, 2005).

Management of marine NIS should be primarily focussed on managing invasion vectors and pathways, as eradication of the already invaded NIS has been proven mostly impossible in the marine environment (Ojaveer et al., 2014; Lehtiniemi et al., 2015 and references therein). Amongst invasive fish, information of their transport and release are the least investigated aspects and therefore research on the transport and dispersal should be prioritized (García-Berthou, 2007). Our results indicate, that the combination of long-distance dispersal (evidenced as shipping as a significant factor in the MaxEnt models) and short-distance spread from the shipping hotspots explain the current pattern of round goby observations in the Baltic Sea. The round goby is classically considered as a demersal fish throughout its life cycle. However, recent evidence suggest that this might not be completely true, as diurnal vertical migration of both fish larvae and early juveniles was observed occurring in the pelagic zone during the night (Hayden and Miner, 2009; Hensler and Jude, 2007). This is important especially from management perspective: if ships were ballasting their tanks near the surface only during daylight, it may have reduced further spread of the fish in the Baltic Sea and elsewhere.

The round goby has high potential for secondary spread. In the Great Lakes the round goby was initially expected to remain within rocky habitats but in just 5 years after the first appearance, the invasive fish colonized all the lakes, with the exception of a large part of Lake Superior (U.S. Geological Survey, 2015), and is currently expanding its distribution upstream in adjacent rivers (Bronnenhuber et al., 2011). The range expansion has been much slower in the Baltic Sea where a pan-Baltic spread was reached in about two decades. The round goby has invaded the Baltic Sea probably already in late 1980's, but only very recently significantly expanded its range in several localities, mostly to port and harbour areas. To date, there are still several ecologically suitable areas which have remained uncolonized (*e.g.*, west coast of the Baltic Sea) or where the abundance remains relatively low. Such slow colonization could be attributed either to a broad range of environmental conditions of the Baltic Sea or a low genetic diversity of the round goby, described from haplotype analysis (Grigorovich et al., 2003a). Puck Bay in the south-eastern Baltic Sea was suggested to be the primary invasion site in the Baltic Sea (Björklund and Almqvist, 2010). However, due to our limited knowledge it cannot be concluded whether there has been only one primary invasion or multiple invasions from different source populations as has taken place in the Great Lakes (Brown and Stepien, 2009; Björklund and Almqvist, 2010). Nevertheless, temperate high-productivity brackish water seems to be a very favourable habitat for the round goby as the species exhibits longer lifespan and larger individual sizes in the Baltic Sea compared to their native distribution area (Sokołowska and Fey, 2011). Only the northernmost areas of the Baltic Sea, like Bothnian Bay, might likely pose difficulties for the round goby due to too extreme thermal conditions. However, our MaxEnt models did not indicate this restriction (see also Fig. 1).

In conclusion, the models used in this study provide valuable insights to roles of different environmental variables determining the round goby's distribution in the Baltic Sea. Potentially the models can be applied to predict future distribution trends of this species if used with caution. The models demonstrate clearly that the spatial distribution of the round goby in the Baltic Sea is a function of shipping intensity (distance to port, cargo traffic) and abiotic hydroclimatic environment (wave exposure). Although high frequency of release does not necessarily lead to successful invasions, the round goby seems not to have major environmental constraints in the Baltic Sea. This points to an obvious need for effective management measures of the Baltic shipping, including performing relevant risk assessments in intra-Baltic shipping (*e.g.*, David et al., 2013).

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