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Marine protected areas modulate habitat suitability of the invasive round goby (*Neogobius melanostomus*) in the Baltic Sea

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ABSTRACT

Biological invasions are one of the leading causes of biodiversity loss worldwide. Given that eradication of invasive species is not usually a practical option, conservationists may attempt to limit their impacts through the designation and management of protected areas. Here, we investigate the effect of marine protected areas on the habitat suitability of an invasive species, the round goby (*Neogobius melanostomus*). By modelling its environmental niche space in the Baltic Sea, we demonstrated that gobies prefer shallow, warmer waters, sheltered from significant wave action. They are more likely to be found near areas of intense shipping, this being their primary method of long-distance dispersal. Comparison of the goby's occurrences inside/outside protected areas indicated that suitable habitats within protected areas are more resistant to the round goby's invasion compared to adjacent unprotected areas, however the opposite is true for suboptimal habitats. This has important ecosystem management implications with marine conservation areas providing mitigation measures to control the spread of round goby in its optimal habitats in the Baltic Sea environment. Being subjected to reduced human impacts, native species within protected areas may be more numerous and diverse, helping to resist invasive species incursion.

1. Introduction

Invasive species are one of the greatest threats to biodiversity worldwide (Clavero and García-Berthou, 2005). The arrival of an alien species into an ecosystem often results in rapid and dramatic changes in species composition, as the alien species competes with, preys on, or parasitizes endemic species (Clavero and García-Berthou, 2005; Jeschke, 2014; Gallardo et al., 2016). Species diversity may be reduced, leaving the invaded area more vulnerable to additional invasive species (Stachowicz et al., 1999). Anthropogenic habitat disruption or destruction may increase the risk of biological invasion and, as many alien species are introduced via human activities, biological invasions are becoming more common and more likely to be successful (Leppäkoski and Olenin, 2000; Hulme, 2009). Given the threats posed by invasive species and as the global impacts of human activity continue to grow in severity, it is imperative that they are suitably managed (Halpern et al., 2008).

To date, the majority of studies overlook invasive species in conservation planning (Mačić et al., 2018), despite it being practically impossible to remove an invasive species, unless it is detected early in the invasion process ansd decisive action is swiftly taken (Bax et al., 2003). Management of invasive species, limiting their spread and impacts, is often the only possible course of action, and effective management strategies are of great importance. However, there exist only a few case studies where such mitigation measures have been proposed (Mačić et al., 2018). Designated protected areas are a key tool with which conservationists try to protect native species and sensitive habitats, but that can also serve to limit invasive species. When biological invasions occur, they are often in ecosystems that are degraded and compromised by human activity, and so designated protected areas, which are typically less disturbed, may offer resistance against an invasive species (Chape et al., 2005; Gallardo et al., 2017). Species richness may be greater in protected areas, leaving few unoccupied niches within the ecosystem for the invader to fill, making it harder for it to become established (Stachowicz et al., 1999; Edgar et al., 2014; Kelaher et al., 2014). These protected areas may harbour more stable predator populations that can impose top-down control on the invader before it becomes established, or keep the invasive population at a low

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level (Sakai et al., 2001). Similarly, protected areas may possess a greater abundance and/or diversity of native competitor species that may also limit the invader's success (Jeschke, 2014). Studies of invasive species within protected areas, however, do not always show this resistance effect. In some cases, invasive species also benefit from protection from human activities, allowing them flourish more than they otherwise would (Burfeind et al., 2013; Mačić et al., 2018). Hence, for protected areas to continue being an important part of conservationists' toolkit, their relationship to various invasive species warrants further attention.

The round goby (*Neogobius melanostomus*) is listed as one of the "100 Worst Invasive Species in Europe" (Vilà et al., 2009). It is a small, benthic fish, native to the Ponto-Caspian region, and has spread via ballast water around Europe and to the North American Great Lakes (Corkum et al., 2004). Within the Baltic Sea, where it arrived approximately 25 years ago in the Gulf of Gdańsk, it has rapidly spread across the Baltic Sea within this period (Ojaveer, 2006; Kornis et al., 2012; Azour et al., 2015; Behrens et al., 2015; HELCOM, 2018). The round goby is a euryhaline, eurythermic, fast-breeding, and aggressive species, with a highly generalist lifestyle, all of which help make it an excellent invader (Corkum et al., 2004; Kornis et al., 2012). The round goby is a strong competitor that preys on many benthic species and, in many areas of its invasion, it has become overwhelmingly dominant, drastically altering local ecosystems (Kornis et al., 2012; Rakauskas et al., 2013). Future colonisations via ballast water as a vector are possible, although recently implemented ballast water management strategies may help to prevent this (Gollasch and Leppäkoski, 2007; IMO, 2017). The larvae are nocturnally pelagic, where they predate on zooplankton, which is likely how they have been pumped into ballast water and translocated to new areas (Hensler and Jude, 2007; Kornis et al., 2012; Jůza et al., 2016). The round goby is capable of thriving in waters between 0 and 30 °C, although anthropogenic climate change is likely to intensify the round goby's invasive capabilities, as new areas are warmed to suitable levels and its temperature-dependant reproductive cycle allows it to breed more often in warmer environments (Occhipinti-Ambrogi, 2007; Houston et al., 2014).

The rapid spread of the round goby in the Baltic Sea is unsurprising, given how suitable the biogeography of the area is: the Baltic Sea is a large, shallow body of water characterised by low salinity and cold temperatures (Walday and Kroglund, 2002). The area shares many features with the round goby's native range in the Black and Caspian Seas, and round gobies are highly successful in freshwater and brackish areas, like the Baltic and its surrounding rivers and lakes (Leppäkoski and Mihnea, 1996; Paavola et al., 2005; Sokołowska and Fey, 2011). The Baltic Sea has already been the site of many biological invasions, and the ecosystem disruption caused by these may make it more vulnerable to further invasion, which may also contribute towards the success of the round goby (Leppäkoski and Olenin, 2000; Leppäkoski et al., 2002).

The round goby has become an important prey species for many species native to the Baltic Sea. Fish species such as perch, cod, and zander are known to prey on the round goby, as well as birds such as herons and cormorants (Pachur and Horbowy, 2013; Rakauskas et al., 2013; Hempel et al., 2016; Liversage et al., 2017; Mikl et al., 2017; Oesterwind et al., 2017). Marine protected areas (MPAs) may display greater biodiversity than adjacent seas, either because they are selected for their significant biological diversity, and/or because they are managed to allow local species reprieve from human activities (Halpern, 2003; Guidetti, 2006; Fraschetti et al., 2013). It is likely that predatory control of gobies is more intense in MPAs which provide refugia for these predator species (Kornis et al., 2012). In these areas, stronger interspecific competition may also play a role in limiting the round goby (Edgar et al., 2014). However, it has been shown to be an aggressive competitor, capable of outcompeting native species for prey, leading to doubt as to whether competition will prevent new invasions (Rakauskas et al., 2013).

This study aims to test whether the presence of the round goby in the Baltic Sea is modulated by MPAs, taking into account the heterogenous environment and the effect of habitat suitability. According to the biotic diversity and predator control hypotheses outlined above, we expect that protected areas will contain fewer round goby occurrences than unprotected areas with similar habitat characteristics, due to stronger interspecific interactions with predators and competitors that prevent the establishment of the round goby. Prior studies have demonstrated that a large part of variability in the distribution of the round goby is explained by salinity, depth, wave action, shipping (propagule pressure), sediment types, and temperature (Kotta et al., 2016; Behrens et al., 2017; Florin et al., 2017; Liversage et al., 2017). In this study, we suggest that protected areas are an important control of invasive species establishment by modulating the response of round goby to other environmental drivers. The results of this study will give further insight into whether MPAs are a useful tool in controlling the round goby and thereby aid in management of this invasive species (Samson et al., 2017).

2. Methods

2.1. Goby occurrence data

The study area consisted of the entire Baltic Sea. Presence-only data, used to model the habitat suitability of the Baltic, was available from a range of sources and consisted of 459 sites (Table 1 and Appendix 1). Presence/absence data, used to contrast the probability of occurrence inside and outside protected areas, was available for two areas in the Baltic Sea. 75 absence sites and 29 presence sites from around the coast of Blekinge, Sweden, were taken from Florin et al. (2017). This data was complemented by the author's (Kotta's) own data of 61 absence sites and 85 presence sites from the coastal waters around Estonia (the Estonian Marine Institute database), totalling 250 presence/absence coordinates (Appendix 2). 94 presence/absence sites were found within protected areas, and 156 in unprotected areas. The GBIF (Global Biodiversity Information Facility) database is based on public reports of occurrences and, as such, may be less reliable than other, published, sources used. The round goby is a visually distinctive species in this region, although the possibility of false reports still exists. Sources from publications are verified by specialists and are less likely to contain false positives.

2.2. Environmental predictor variables

The choice of environmental variables was based on existing knowledge of the factors influencing the distribution of the round goby. Prior studies have demonstrated the importance of salinity, depth, wave action, shipping (propagule pressure), sediment types, and temperature on the distribution of the round goby, (Kotta et al., 2016; Behrens et al., 2017; Florin et al., 2017; Liversage et al., 2017). In addition to these environmental variables, bottom current was included, as the benthic gobies may respond more strongly to directional underwater currents

Table 1
Sources of round goby occurrence data used in this study. Date indicates the collection period.

Source	Date	Number of Occurrences
Florin et al., 2017	2008–2014	29
GBIF, 2018	2009–2018	82
Kotta (personal data)	2015–2017	85
Kotta et al., 2016	2000–2015	239
Ojaveer, 2006	2003–2006	2
Rakauskas et al., 2013	2007–2012	5
Thorlacius et al., 2015	2013–2014	1
Wandzel, 2000	1999	16

Table 2
Sources and details of predictor variables used. Units abbreviations are as follows: ms-1 = velocity in metres per second; psu = salinity in practical salinity units; chlorophyll index = a relative measure of chlorophyll concentration; m = distance in metres; shipping density coefficient = number of ships passing through each cell of the study area within a year; K = temperature in Kelvin.

Variable	Unit	Type	Collection Date	Source	Original Resolution (m)
Bottom Current	ms^{-1}	Continuous	2003–2004	HELCOM	200
Bottom Salinity	psu	Categorical	1999–2004	HELCOM	200
Chlorophyll-a Concentration	index	Continuous	2003–2011	HELCOM	1000
Depth	m	Continuous	2013	BSHD	500
Seabed Sediments	-	Categorical	2007	HELCOM	200
Shipping Density	coefficient	Continuous	2016–2017	HELCOM	1000
SST	K	Continuous	2008–2017	DMI	1100
Wave Exposure	m^2s^{-1}	Continuous	2002–2007	Aquabiota	25

than surface wave action. Chlorophyll-a concentration was used as a proxy for primary production, including the cover of benthic vegetation.

Sea surface temperature (SST) and wave exposure data were acquired through personal communication with the Danish Meteorological Institute (DMI) and Aquabiota Water Research respectively, while the rest of the environmental predictor data was accessed using the Helsinki Commission's (HELCOM) map and data service. See Table 2 and Appendix 3 for details on each variable.

The values of the annual mean bottom current velocity were produced by the Danish National Environmental Research Institute (NERI) for the BALANCE project using the COHERENS model (Bendtsen et al., 2007; Luyten et al., 1999). The annual mean bottom salinity was produced by NERI for the BALANCE project, and consists of six salinity categories: oligohaline I (< 5 psμ), oligohaline II (5–7.5 psμ), mesohaline I (7.5–11 psμ), mesohaline II (11–18 psμ), polyhaline (18–30 psμ), and euhaline (> 30 psμ) (Bendtsen et al., 2007). The depth was produced by the Baltic Sea Hydrographic Commission using numerous interpolated depth grids from a range of countries around the Baltic Sea (Baltic Sea Hydrographic Commission, 2013). Certain areas showed the depth as being above sea level due to imperfect interpolation in low-resolution areas, and goby depth values in those areas were truncated to 0 m. The chlorophyll-a concentration measurements were produced by HELCOM, and combines Medium Resolution Imaging Spectrometer (MERIS) satellite readings from the Finnish Environmental Institute and the Joint Research Centre databases. The data is provided in the form of an index, ranging from 0 to 1 (HELCOM, 2017a). Seabed sediment types were produced as part of the BALANCE project and consisted of bedrock, hard bottom complex (ranging from coarse sand to boulders), sand, hard clay, and mud categories (Al-Hamdani and Reker, 2007). The shipping density raster was produced by HELCOM using Automatic Identification System data. All ships with an International Maritime Organisation number within the Baltic sea were used, and the density represents the number of trips across each cell of the grid (HELCOM, 2017b). SST data, based on a combination of satellite and in-situ recordings, was created by taking a ten-year average (2008–2017) of the average monthly temperature across the Baltic Sea. The data was provided by the DMI (Høyer and Karagali, 2016). Wave exposure data was produced by Aquabiota, using the Simplified Wave Model method (SWM). This incorporates wind data from a number of different monitoring stations around the Baltic Sea to calculate surface wave exposure levels (Wijkmark and Isæus, 2010).

The polygons of Baltic Sea protected areas (HELCOM MPAs and Ramsar sites), used in the evaluation of the effects of protected areas on goby occurrence, were obtained from HELCOM map and data service (HELCOM, 2017c). All environmental data were modified to have the same resolution and extents and ETRS-89 LAEA coordinate reference system was used.

2.3. Habitat suitability

MaxEnt was used to model the habitat suitability of the round goby within the heterogenous environment of the Baltic Sea. MaxEnt is a machine learning program which uses presence-only data and is a form of species distribution modelling (SDM) that is frequently used when predicting potential distribution of invasive species, as species absences are rarely recorded and therefore presence-absence modelling techniques cannot be used (Phillips et al., 2004; Elith et al., 2011; Guisan et al., 2013). MaxEnt, unlike many SDM techniques, is able to make use of presence-only data when training the model, by creating artificial absence data, termed pseudo-absences (Barbet-Massin et al., 2012). It can produce response profiles to individual predictor variables, giving insight into the conditions that are favourable for the focal species, and the relative importance of each predictor variable in determining habitat suitability. As MaxEnt is known to be prone to overfitting, producing unrealistically-complex responses to environmental variables, the selected model was modified by adding a small "beta" regularisation parameter, which simplifies the variable responses (Warren and Seifert, 2011). Due to the large study area, 10,000 background points were randomly chosen to provide pseudo-absences (Barbet-Massin et al., 2012).

When determining the relative importance of predictor variables, collinearity between variables were first checked, since highly correlated variables can be problematic when modelling using MaxEnt. A Spearman's rank correlation analysis of the predictor variables showed low correlation between almost all variables, with only SST and bottom salinity having a value of greater than ± 0.7 (ρ = 0.815). Nevertheless, this value is below the critical threshold in which collinearity will begin to severely distort model estimations and subsequent prediction (Dormann et al., 2013).

Presence-only data, used for model training, consisted of 459 sites from a range of sources (Table 1). Comparing the environmental variable distributions between presence sites and pseudo-absence sites showed no notable differences, therefore sampling bias was considered problematic (Kotta et al., 2016). For each presence record and randomly generated pseudo-absence/background point, the values of the predictor variables at those coordinates were extracted, which were used to create the MaxEnt model. Since many individuals were found close to the coastline, it was not always possible to directly obtain predictor variable data from the goby coordinate data, due to certain datasets limited resolution and coverage. Rather than discounting these data points, which would have significantly limited the analysis, as different individuals were lacking different variable data, the values of the background variables were estimated using the "fill no data" function in QGIS (QGIS Development Team, 2018). The function fills regions with missing values by interpolating outwards from areas with data using inverse distance weighting. The intention of this analysis was

Table 3
Variable importance of predictor variables for determining habitat suitability of the round goby. Both percent contribution and permutation importance are created by randomly altering the variable values at training points and measuring the resulting drop in AUC. Percent contribution is produced during the process of model creation and is dependent on the order that variables are added. Permutation importance is calculated after the model is created and is the preferred method of judging variable importance. "AUC only" and "AUC without" columns were produced using a jackknife test of variable importance. "AUC only" levels refer to the AUC of the model if it were based only on that variable, and "AUC without" levels refer to the AUC of the model if that variable is removed.

Variable	Percent contribution	Permutation importance	AUC only	AUC without
Bottom Current	0.2099	0.9414	0.6765	0.9393
Bottom Salinity	5.4839	7.2807	0.6196	0.9379
Chlorophyll-a Concentration	0.719	1.1633	0.8015	0.9385
Depth	44.7835	38.8453	0.8979	0.9318
Sediment type	1.2245	0.8296	0.6676	0.9398
Shipping Density	2.2558	3.0947	0.6827	0.9371
SST	13.4735	17.7836	0.7805	0.9326
Wave Exposure	31.85	30.0614	0.8876	0.9320

to determine broad scale habitat suitability, and predictor variables generally varied over a large scale, rather than locally. There is precedent for this kind of data manipulation, where individuals slightly outside the range of the predictor data have been relocated in order to be used (Florin et al., 2017). Presence records were inspected individually and checked visually to determine whether background variable extrapolation seemed reasonable. Individuals with excessively compromised background variables or whose coordinates placed them on land were excluded (a total of 116 individuals removed).

MaxEnt calculates responses of the focal species to each environmental variable, which can be interpreted as relative probability of goby occurrence. These responses are applied to the study area in order to produce a map of habitat suitability, or relative probability of goby presence, based on local predictor variable values. Areas with higher values are more suitable for round gobies, and possess habitat characteristics that are positively associated with round goby presences. Threshold values are used to provide a more-easily understood prediction, providing a lower limit of habitat suitability, below which is deemed "unsuitable". Choice of threshold is subjective, and other thresholds may be more valuable in different situations (Liu et al., 2013) Here, a logistic threshold based on 10th percentile training threshold, which assigns a threshold value based on a 90% correct classification rate of training data, was used. When modelling an invasive species such as the round goby, a pessimistic overestimate is preferable to a conservative underestimate, thus the 10th percentile training threshold was selected over other, more conservative thresholds. Providing an easily-understood map of the potential distribution of the round goby is useful when attempting to help manage its invasion.

Ten-fold cross-validation was used to estimate the uncertainty of the overall model performance and of goby responses to individual background variables. Model selection was performed using Akaike's Information Criterion corrected for small sample size (AICc) comparison, which is the preferred technique for evaluating MaxEnt models, since it penalises the addition of extra predictor variables (Warren and Seifert, 2011).

2.4. The effect of protection

To determine whether protected areas had a significant effect on the current distribution of the round goby, we performed a logistic regression, with habitat suitability (calculated using MaxEnt) and habitat protection status as independent variables and the binomial goby presence/absence data, in the areas that it was available, as the dependent variable. This allowed us to compare the relationship between habitat suitability and the probability of goby presence inside and outside protected areas.

All analyses and data management were performed using R or QGIS (Hijmans and Elith, 2017; Kassambara, 2017; Muscarella et al., 2014; R Core Team, 2017; QGIS Development Team, 2018; Wickham, 2009).

3. Results

3.1. MaxEnt model selection

AICc comparison showed that all variables were beneficial to the model, with the removal of any variable causing an increase in AICc. When considering beta regularisation strength, however, a marginally sub-optimal model was selected (beta multiplier = 2, ΔAICc + 0.993%, from 5181 to 5232). This decision was based on the knowledge that MaxEnt tends to overfit: predictor variable responses may be excessively complex (Warren and Seifert, 2011). This decision may introduce error into the model prediction, however, since one objective of this habitat suitability modelling is to investigate the potential distribution of an invasive species, overfitting limits the predictive ability of the model, so the suboptimal model was deemed acceptable (Radosavljevic and Anderson, 2014). The average area under receiving operating curve (AUC) of each fold of the ten-fold cross-validation was 0.940, indicating a high level of model accuracy.

3.2. MaxEnt results

The MaxEnt procedure returns a jack-knife test of variable importance, which showed that depth contributed the most to the model (i.e. had the most unique information), followed wave exposure, chlorophyll-a concentration, SST, shipping density, bottom current, sediment type, and bottom salinity (indicating that salinity provided the least information that wasn't present in other variables) (see Table 3). Unique information lost by the removal of single variables was minimal (AUC loss of 0.008 or less). The variables, in descending order of importance on the distribution of the round goby, were: depth, wave exposure, SST, bottom salinity, shipping density, chlorophyll-a concentration, bottom current, and sediment type. Bottom current and sediment type contributed less than 1% towards the model (Table 3).

The MaxEnt model indicated that depth, wave exposure, and SST were the most important variables explaining the distribution of the round goby (Table 3). Bottom salinity, shipping density, and chlorophyll-a concentration were of lesser importance, and the effects of bottom current and bottom sediment type were near-negligible. Responses to individual variables (Fig. 1) show that round gobies have high probability of occurrence in shallower areas, with reduced wave action, and higher temperatures. Regarding the environmental variables of lesser importance, increased shipping density and higher levels of primary production are positively associated with round goby presence. Areas with increased bottom current and hard bottom complexes are also positively associated, though their influence is marginal. Round gobies were also less likely to be found in areas between 11 and 30 psu than at other salinities.

The MaxEnt model was applied to the environmental data to create a map of habitat suitability for the whole Baltic Sea (Fig. 2). The 10th percentile training threshold value was 0.1655, indicating that areas with values above 0.1655 are "suitable" for round gobies. The minimum and maximum habitat suitability values produced for the entire Baltic Sea were 2.500×10^{-4} and 0.9248, with 11.08% of the Baltic Sea's area being deemed suitable.

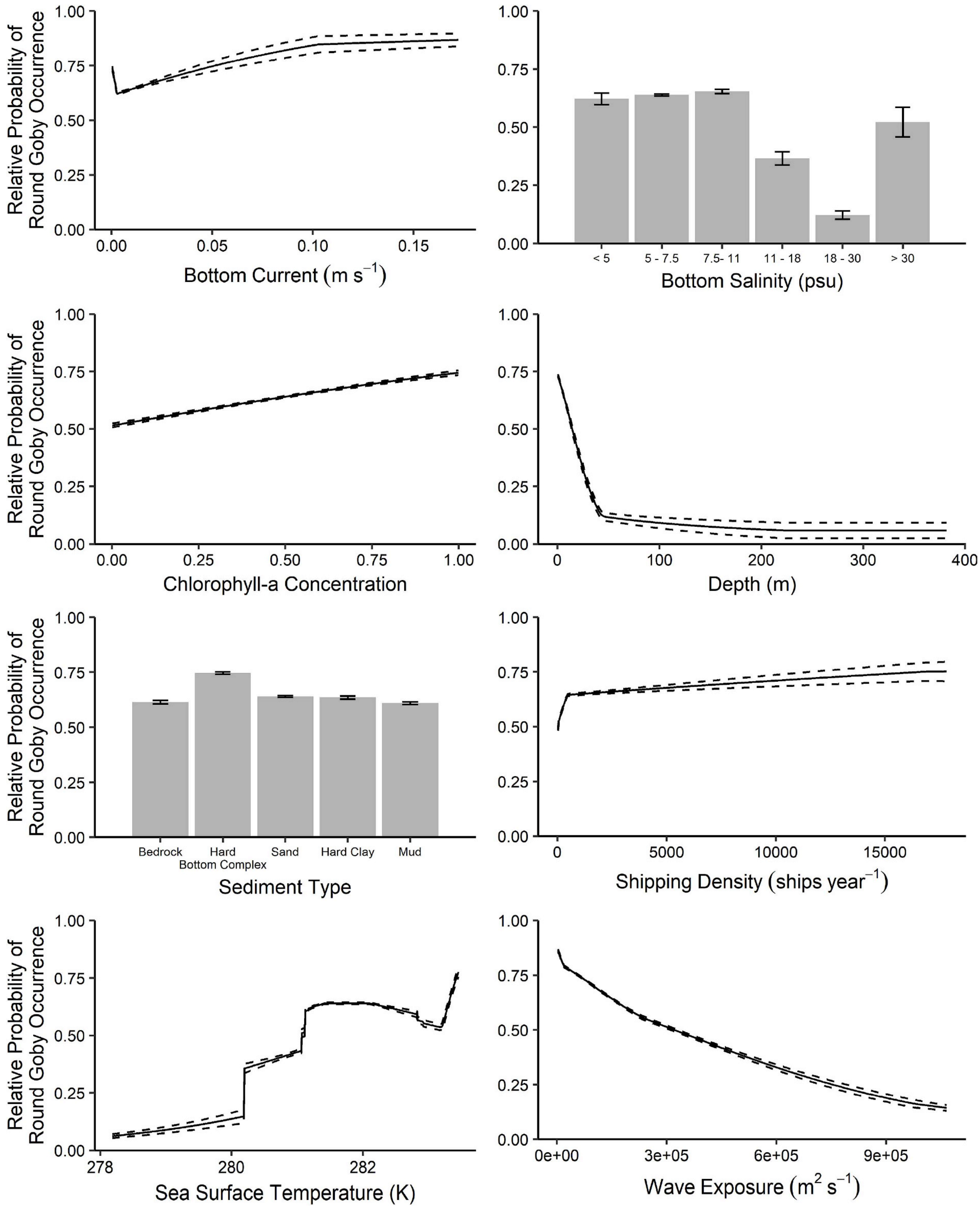

Fig. 1. Responses of the round goby to eight environmental variables. The y-axis is based on a logistic transformation of the raw MaxEnt output, which can be used as a relative probability of round goby occurrence. Error bars and shaded areas represent one standard deviation based on the ten-fold cross-validation.

3.3. The effect of protection

The logistic regression (N = 250) showed highly significant differences ($p < 0.01$) in probability of goby occurrence for all tested variables: protection ($z = -4.079$, $p = 4.53 \times 10^{-5}$), habitat suitability ($z = -2.665$, $p = 7.69 \times 10^{-3}$), and the interaction between protection and habitat suitability ($z = 4.765$, $p = 1.98 \times 10^{-6}$). The relationship between habitat suitability and likelihood of goby occurrence differed between protected and non-protected areas. In unprotected areas, the probability of presence increased with habitat suitability, however, in protected areas, the relationship was inverted: round gobies were less likely to be found in "suitable" areas (Fig. 3).

4. Discussion

This study showed that depth, wave exposure and SST explained the

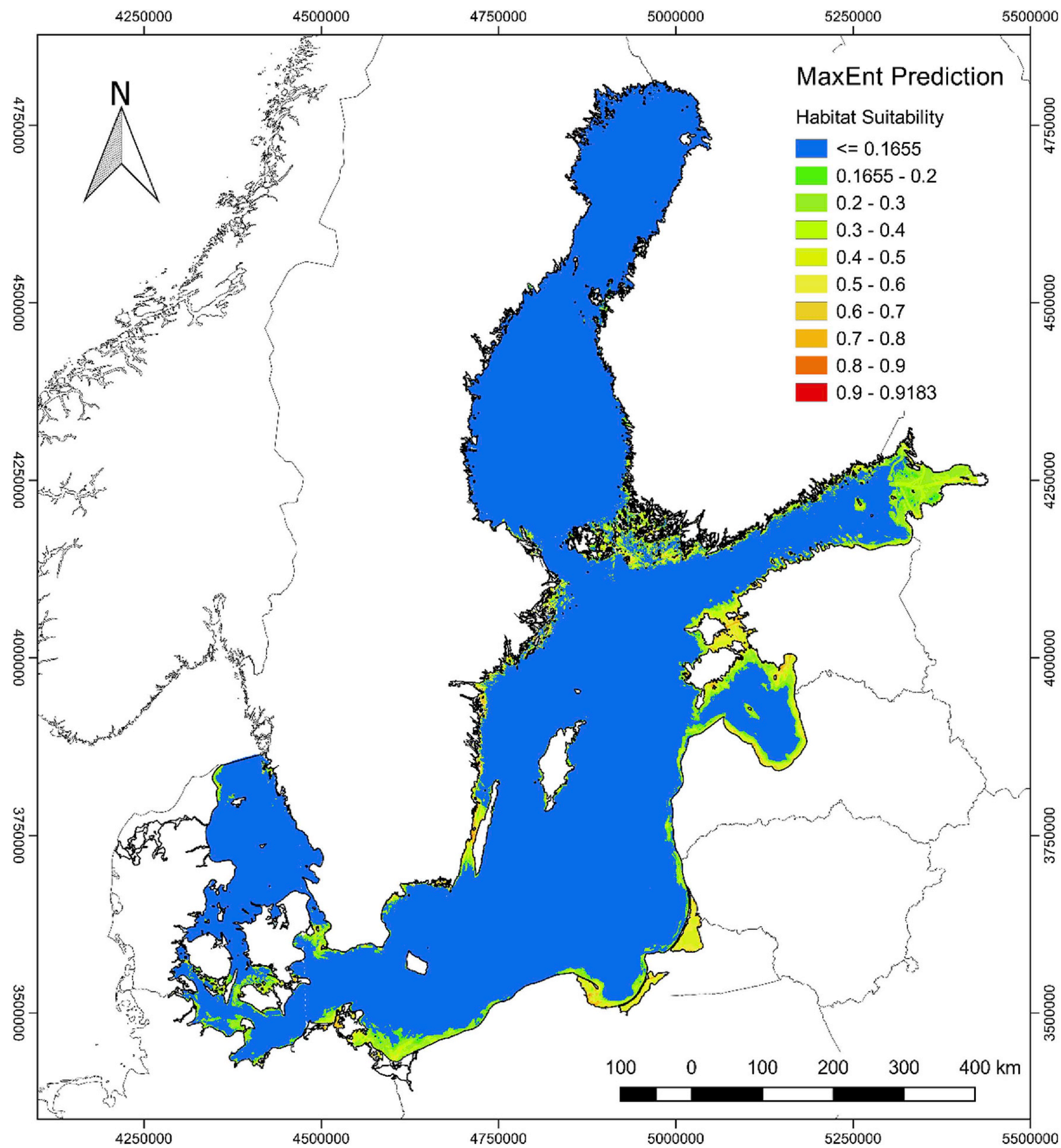

Fig. 2. Habitat suitability for the round goby across the Baltic Sea. All blue areas (suitability ≤ 0.1655) are deemed unsuitable for the round goby, based on the 10th percentile training threshold calculated during the modelling process. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

majority of the probability of occurrence of round goby. Increasing water temperature, chlorophyll-a, shipping density and bottom current velocity increased the probability of round goby while increasing depth, and exposure to waves decreased the probability of round goby in the Baltic Sea area. The round goby is a benthic species that is favoured by warm and productive areas, within shallow waters in the photic zone. The productive areas may provide the round goby with more prey while also sheltering it from predators (Liversage et al., 2017). The round goby shows an affinity towards less exposed shores, sheltered from harsh wave action, where it can conserve energy when maintaining its position on the seabed (Lee and Johnson, 2005). In contrast, round gobies were positively associated with bottom current, which never reaches high enough speeds to be problematic for the round goby and which may aid in juvenile dispersal and supply of food (Tierney et al., 2011; Lechner et al., 2014; Jůza et al., 2016). This preference to high habitat heterogeneity is also reflected by their high affinity to complex hard bottom substrates, characteristic of boulders, coarse sand, and other sediments (Ray and Corkum, 2001; Young et al., 2010; Florin et al., 2017). The round goby is also known to tolerate a broad salinity range (from freshwater to near-oceanic conditions) with little consequence to its fitness (Karsiotis et al., 2012; Behrens et al., 2017). As the majority of the Baltic Sea falls within this salinity range, the contribution of salinity to the MaxEnt model was low. Although the round goby is a demersal fish species, our model made use of surface water temperature (SST) rather than bottom water temperature, mostly because the SST product is of higher resolution and more recent origin. Nevertheless, in the shallow water habitats of the round goby, SST and bottom water temperature are known to correlate highly. While the goby shows a positive association with increasing surface temperature there is likely a slight difference between the temperature measurements used to model habitat suitability and the actual temperatures experienced by the goby.

Protected areas have a notable effect on likelihood of goby occurrence, potentially an encouraging result for conservationists. The MPAs

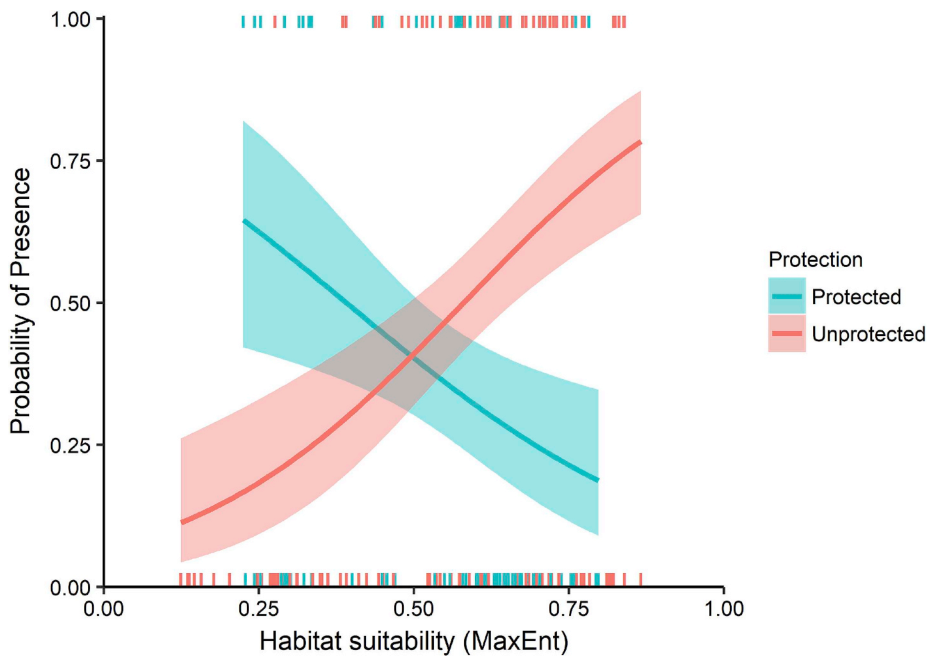

Fig. 3. A comparison of the relationship between habitat suitability and probability of round goby presence in protected and unprotected areas. Records of the habitat suitability of presences (y = 1) and absences (y = 0) used to perform the regression are indicated by vertical lines.

significantly modified the likelihood of round goby presence along the gradient of its habitat suitability. In unprotected areas, likelihood of goby presence increased as habitat suitability increased, whereas in protected areas, the relationship was inverted, and likelihood of goby presence decreased with increasing habitat suitability. Round gobies were more likely to be found in "unsuitable" areas if they are protected and more likely to be found in "suitable" areas if they were unprotected.

A systematically lower probability of round goby occurrence in prime habitats within protected areas suggests that habitat protection hinders the establishment, survival, and/or spread of round goby. As the protected and unprotected areas included in the analysis share similar abiotic environmental conditions, biological interactions are likely responsible for the reduced probability of occurrence, although demonstrating causality was not possible with the available data. Protected areas may be characterized by more heterogeneous seascapes that support more stable populations of top predators (Fraschetti et al., 2013). Anthropogenic pressures, such as fishing activities, on these top predators may also be lower in these areas, thus it is plausible that the round goby will suffer higher losses due to elevated predation in protected areas (Noè et al., 2018). The round goby is already a dominant prey for perch and their contribution in the perch diet has increased over time (Liversage et al., 2017). It has also become of considerable importance in the diets of cod, pikeperch, and pike (Almqvist et al., 2010). Piscivorous birds also benefit from the introduction of round goby. For example, one of Europe's largest heronries occurs in a reserve on the Vistula Spit (Baltic Sea, Poland) and a large *Ardea cinerea* population increase has been linked to the introduction of round goby (Jakubas, 2004). Competition may also hinder the round goby, although it has been shown to be a strong competitor, capable of outcompeting native species by aggression and/or predation (Kornis et al., 2012; Rakauskas et al., 2013). Determining the mechanisms responsible for the results shown is beyond the scope of this study: the conclusions presented here are based on the evidence of the round goby's role as an important prey item in the Baltic Sea, and the knowledge that protected areas may benefit native predators (Lester et al., 2009; Noè et al., 2018; Zupan et al., 2018).

The results suggest that the management of invasive species is highly context-dependent and a simple expansion of protected areas without proper habitat inventories may actually increase a risk of the invasion of round goby. Global conservation targets, such as those found in the Convention of Biological Diversity, prioritise the creation of large protected areas, stating that, by 2020, 10% of marine areas should be managed as protected areas (Tittensor et al., 2014). Percentage area coverage is an overly simplistic goal, and policy-makers may designate certain protected areas in order to meet areal-based conservation targets, rather than based on biological value, and without considering the negative effects that this may have, such as the increased risk of invasive species.

Given that habitat suitability is important when determining the effectiveness of protected areas at resisting round gobies, it is necessary to understand the ways in which individual factors influence the round goby and their predator and competitor species. When considering the effect of invasive species, new protected areas should be designated with care, with consideration given to potential consequences in that area, rather than simply to meet conservation targets. Additional studies, investigating a wider range of areas, comparing the effect of different management strategies on the round goby, and investigating species interactions with the round goby in Baltic Sea MPAs, would be beneficial. Quantification of the abundance/biomass of the round goby across its range in the Baltic Sea would also be a valuable line of research, as analyses built on presence-only or presence-absence data are limited in their usefulness. This is because impacts of the round goby on different ecosystem elements highly depend on the density of invasive fish (Liversage et al., 2017). However, there exists yet no coordinated regionwide monitoring of invasive species in the Baltic Sea range involving proper quantification of round goby.

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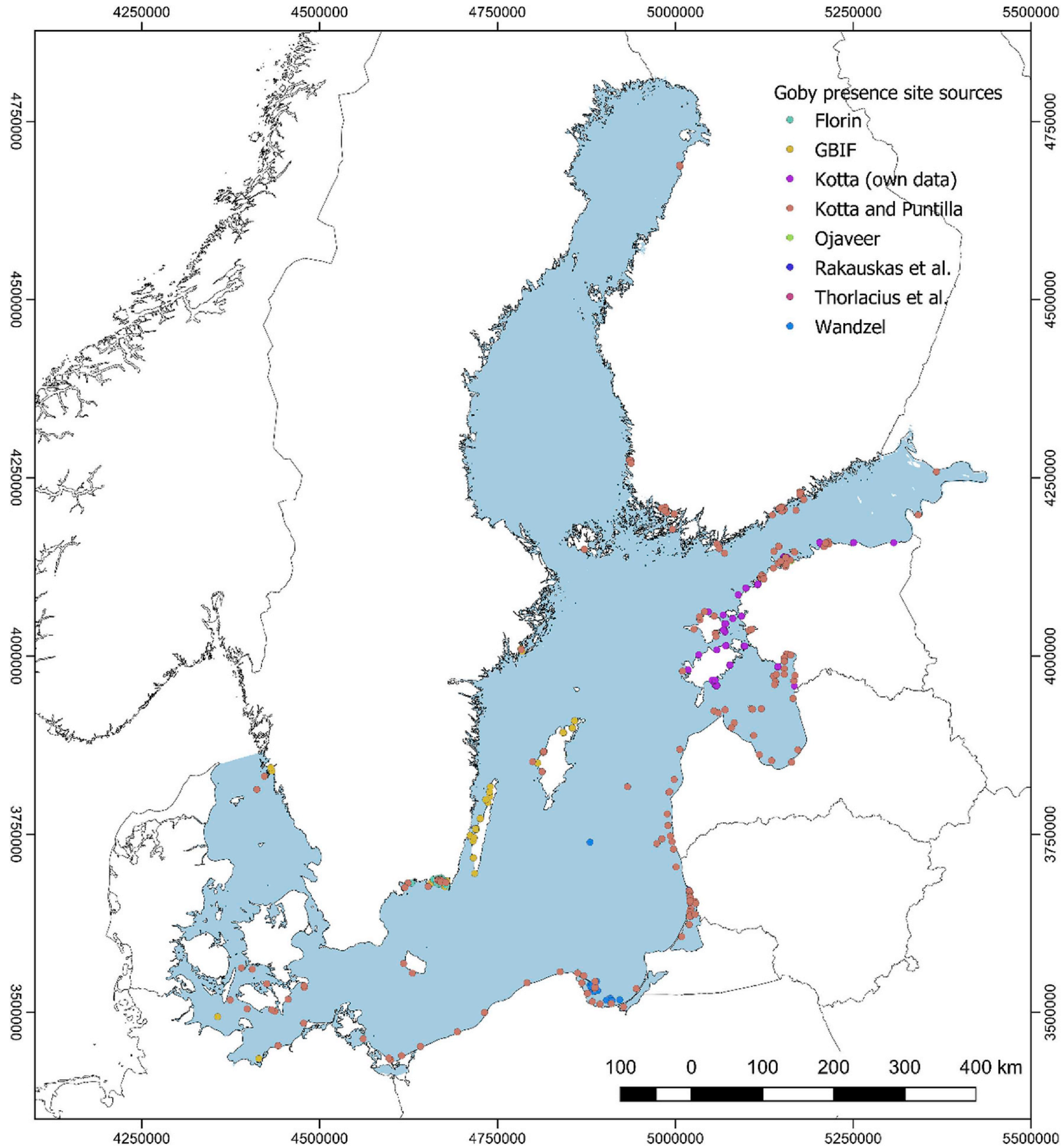
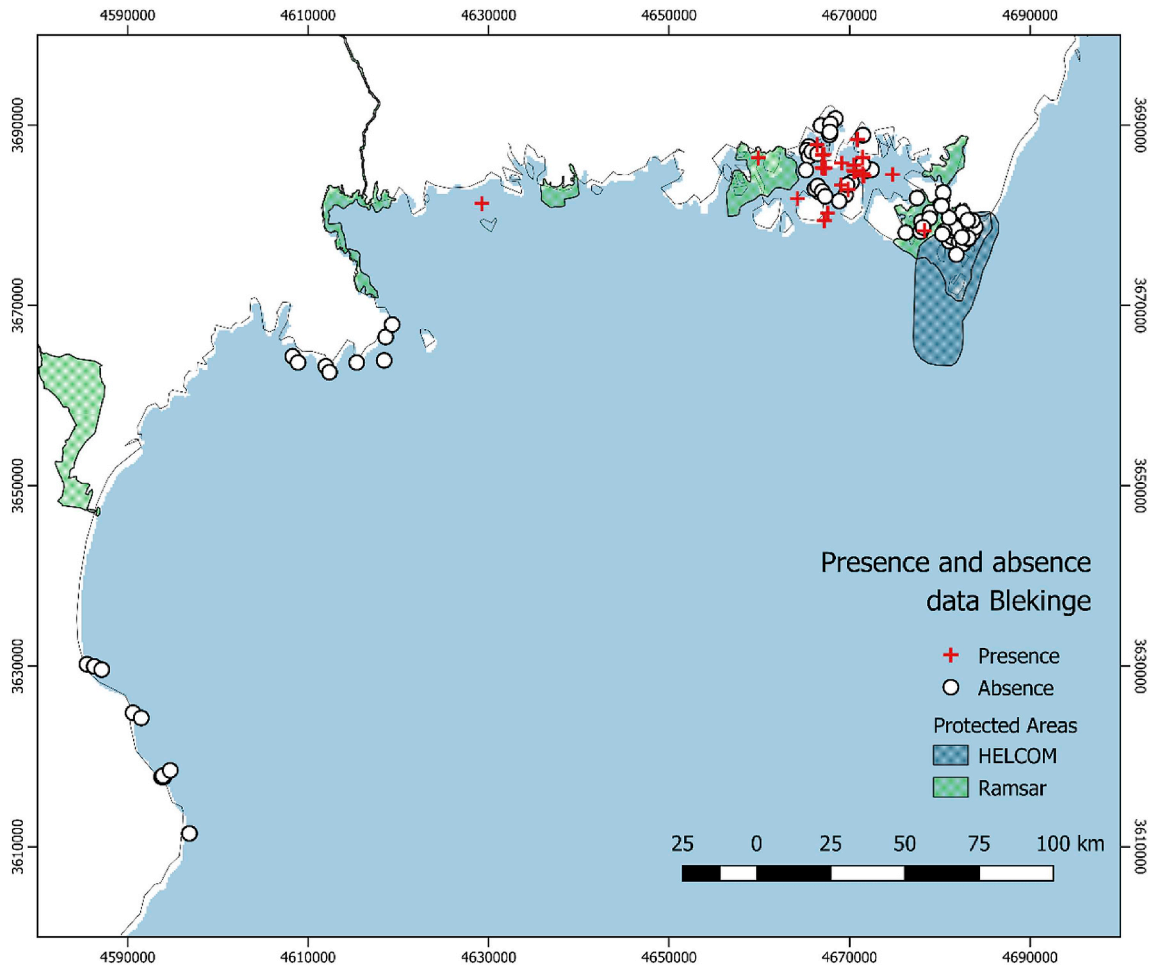
Appendix 1

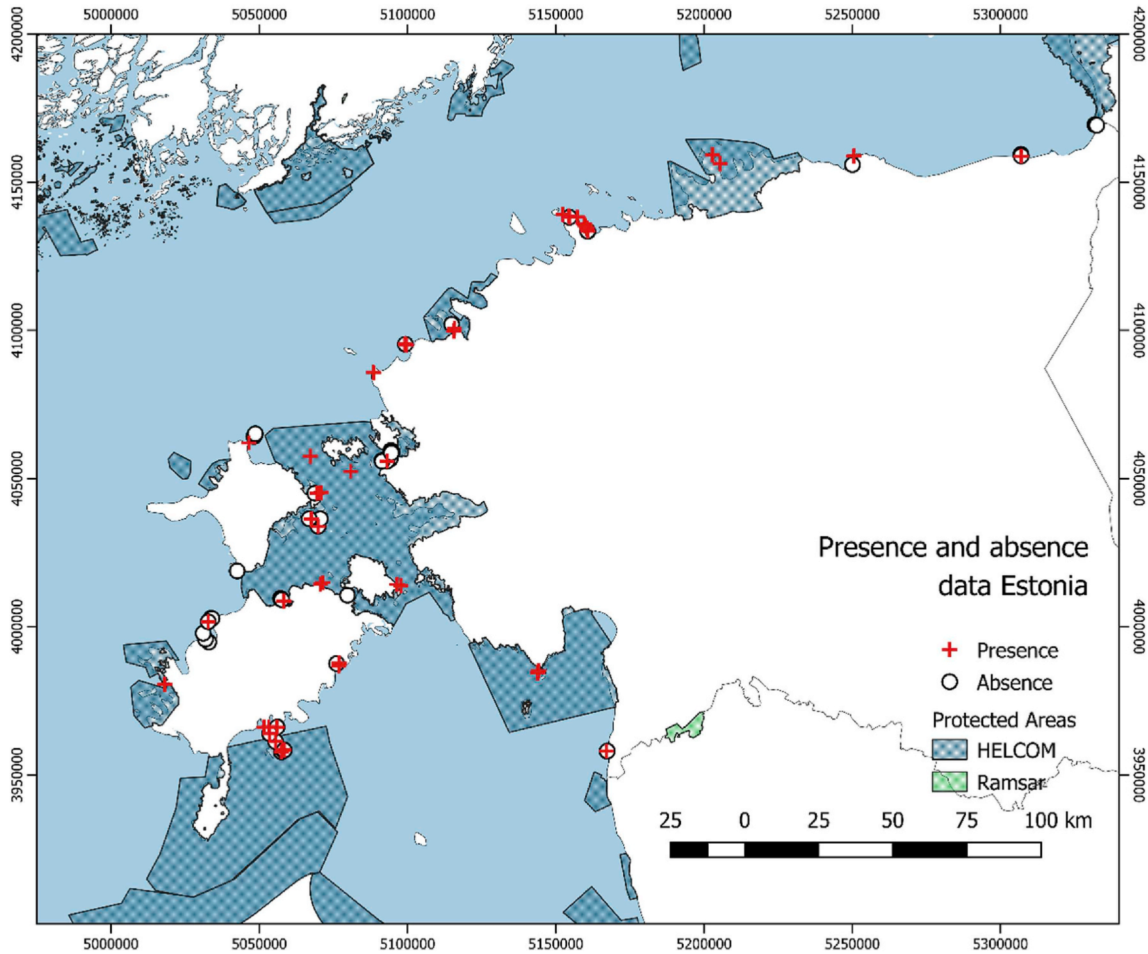


Round goby presence sites and sources in the Baltic Sea.

Appendix 2

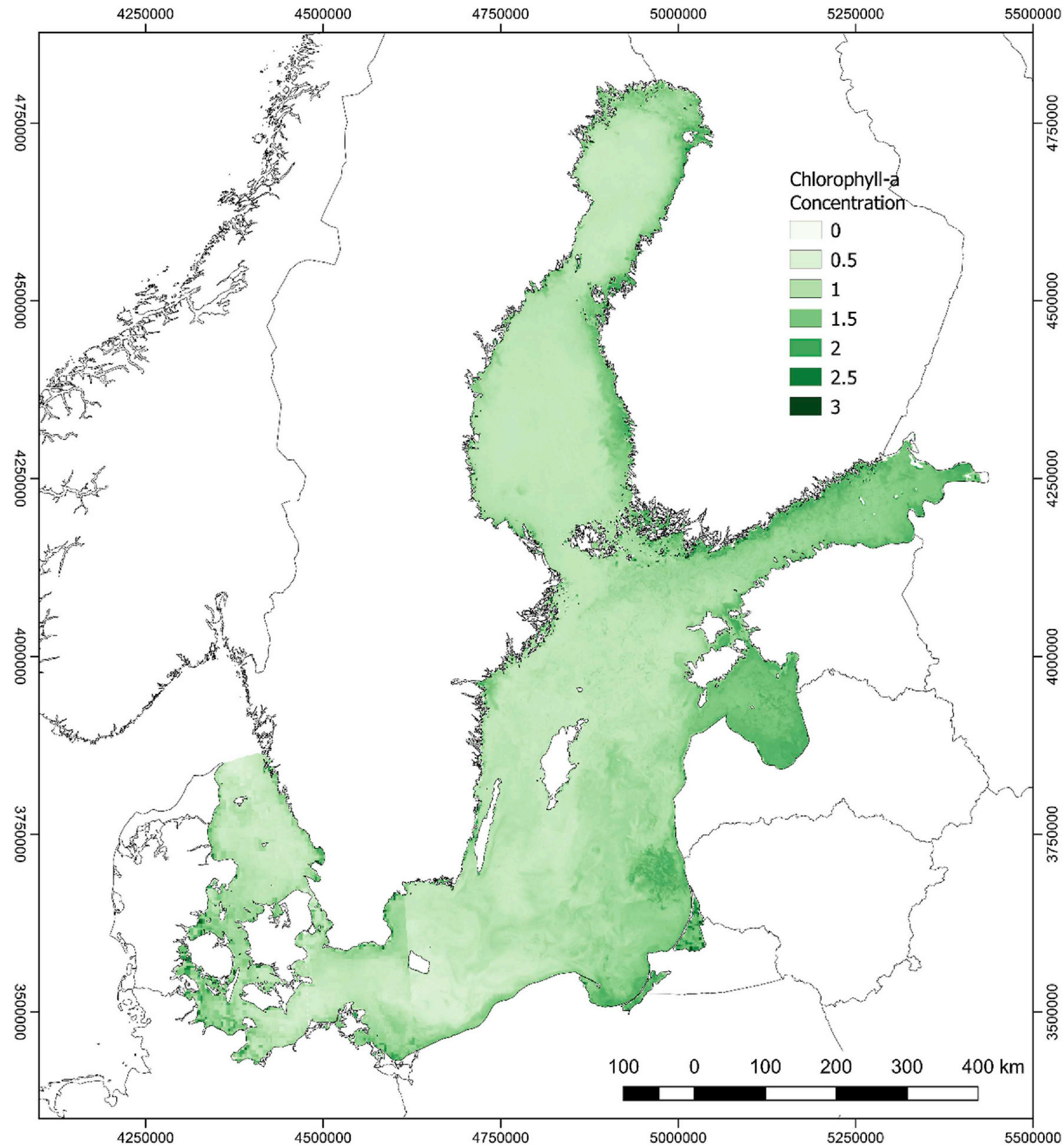


Presence sites, absence sites, and protected areas from the waters near Blekinge, Sweden, used in determining the effect of protection on the distribution of the round goby.

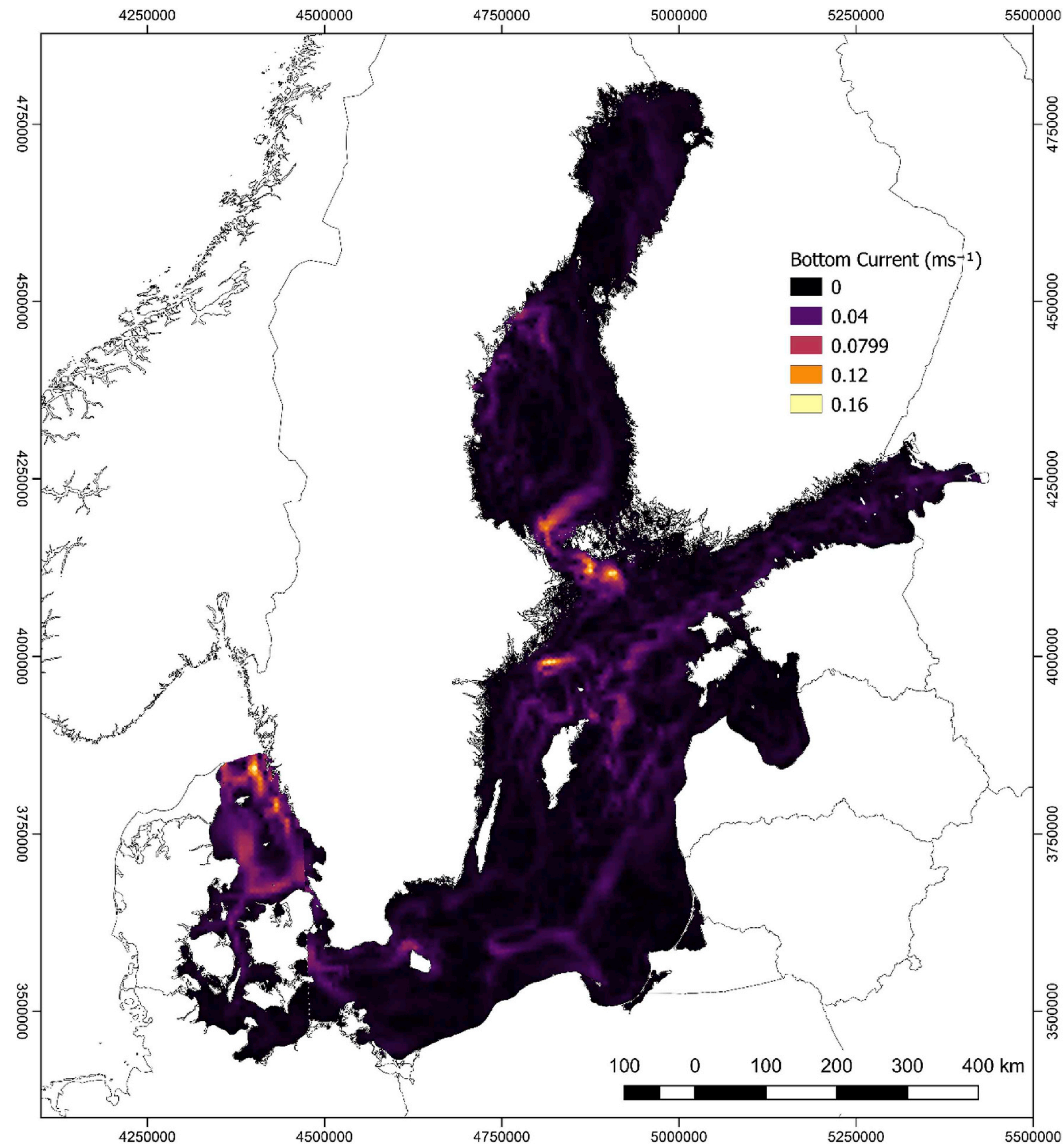


Presence sites, absence sites, and protected areas from the waters near Blekinge, Sweden, used in determining the effect of protection on the distribution of the round goby.

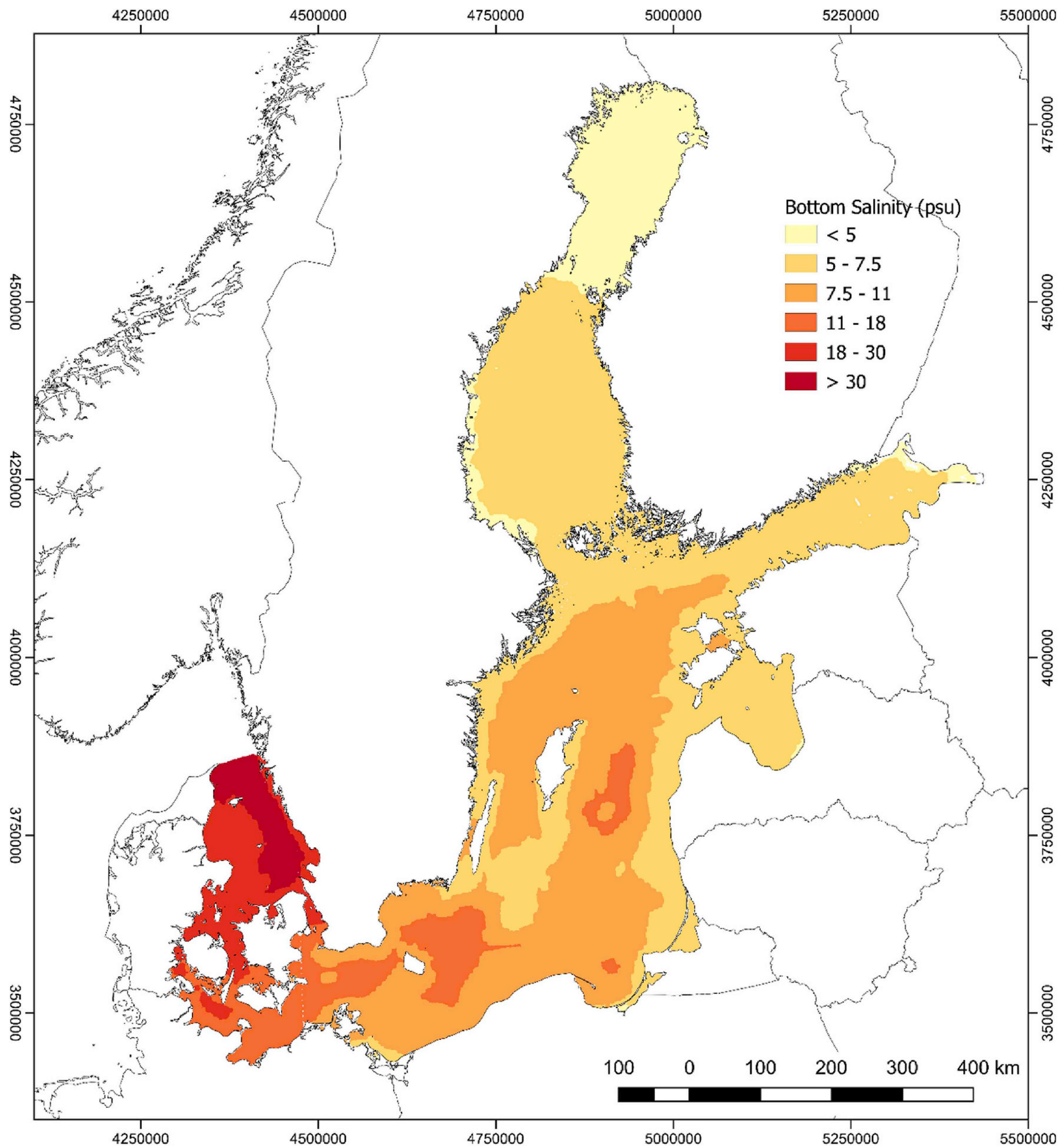
Appendix 3



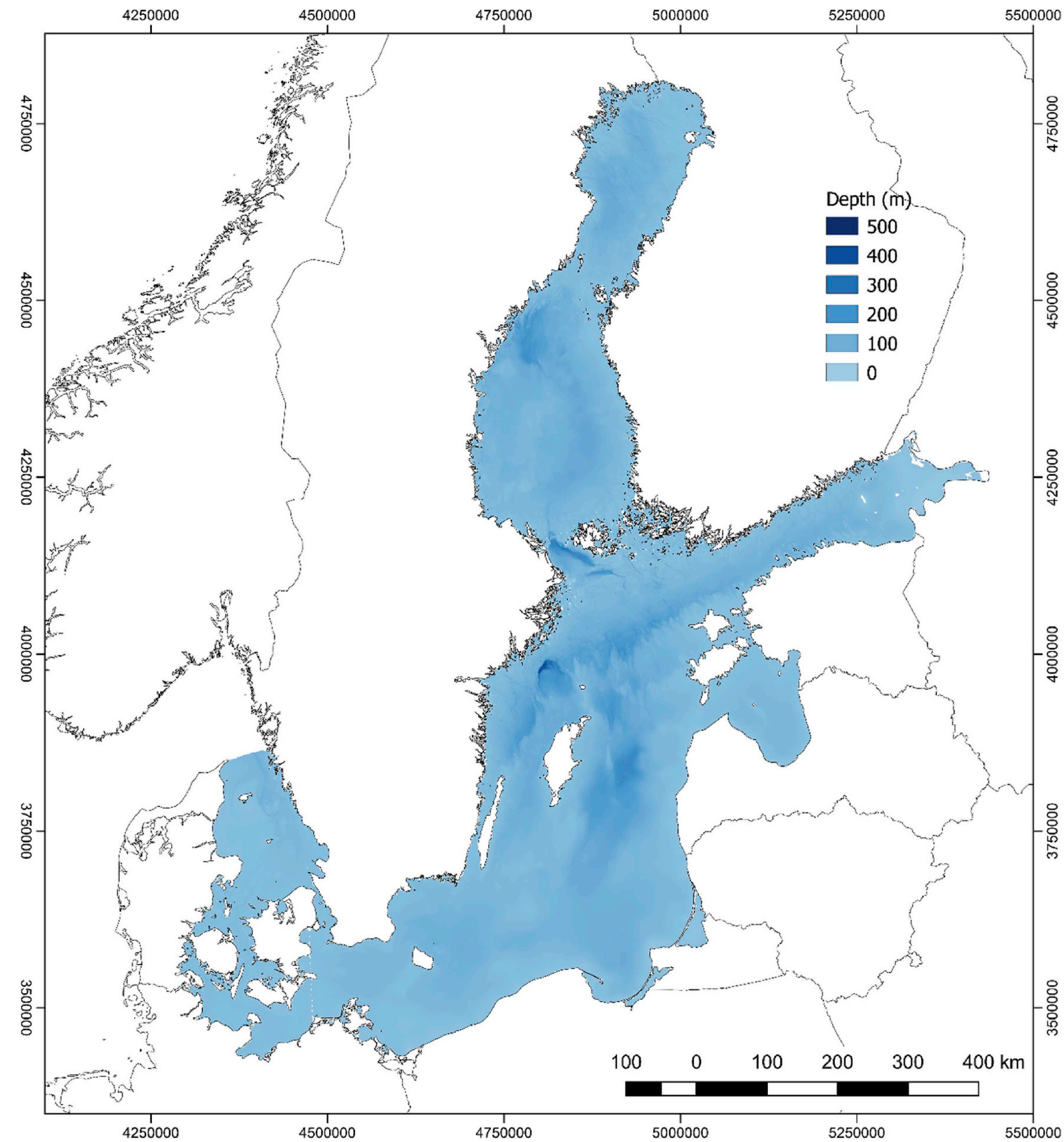
Chlorophyll-a concentration in the Baltic Sea, from HELCOM.



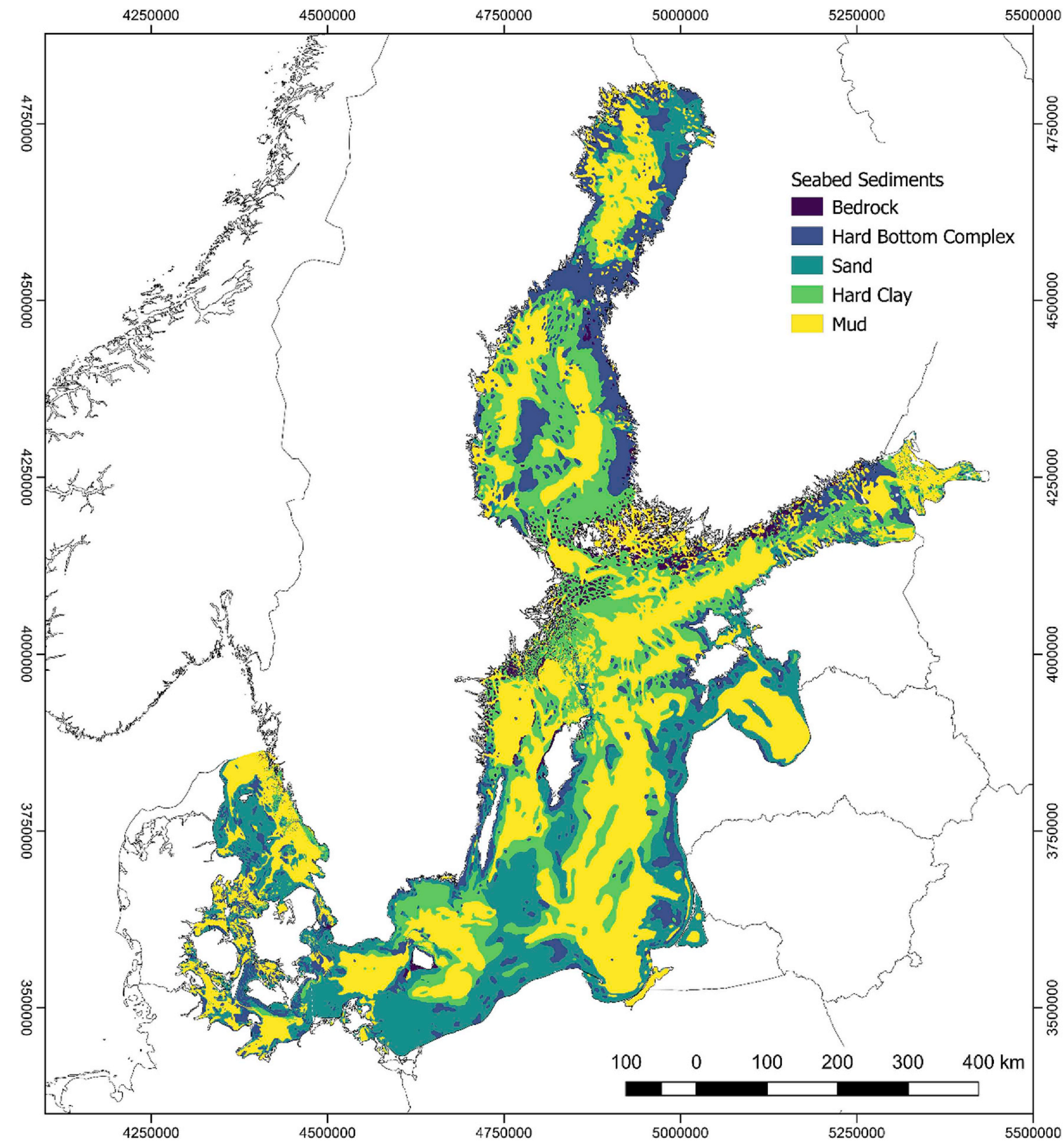
Modelled bottom current in the Baltic Sea, from HELCOM, produced for the BALANCE project.



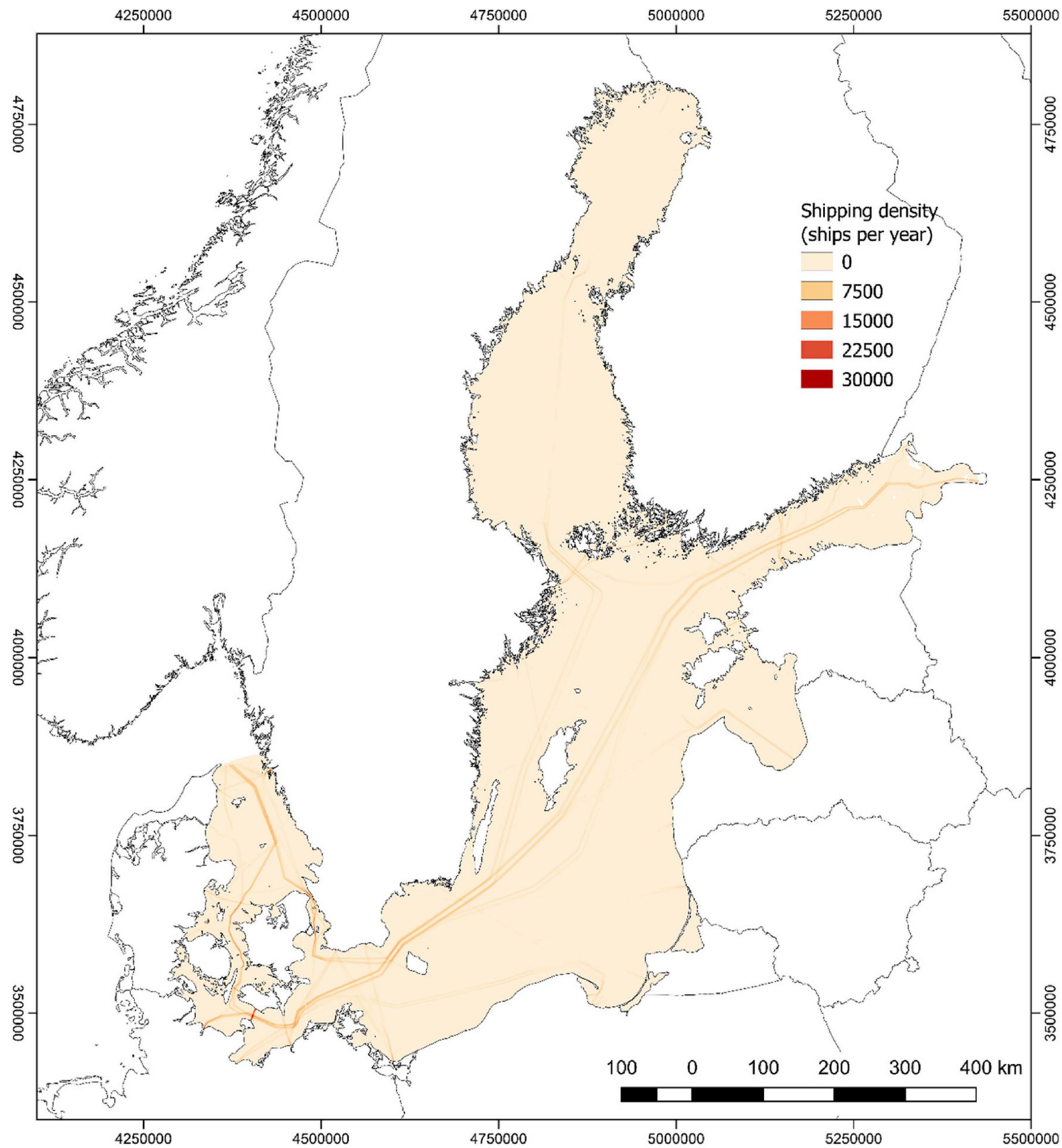
Mean modelled bottom salinity in the Baltic Sea, from HELCOM, produced for the BALANCE project.



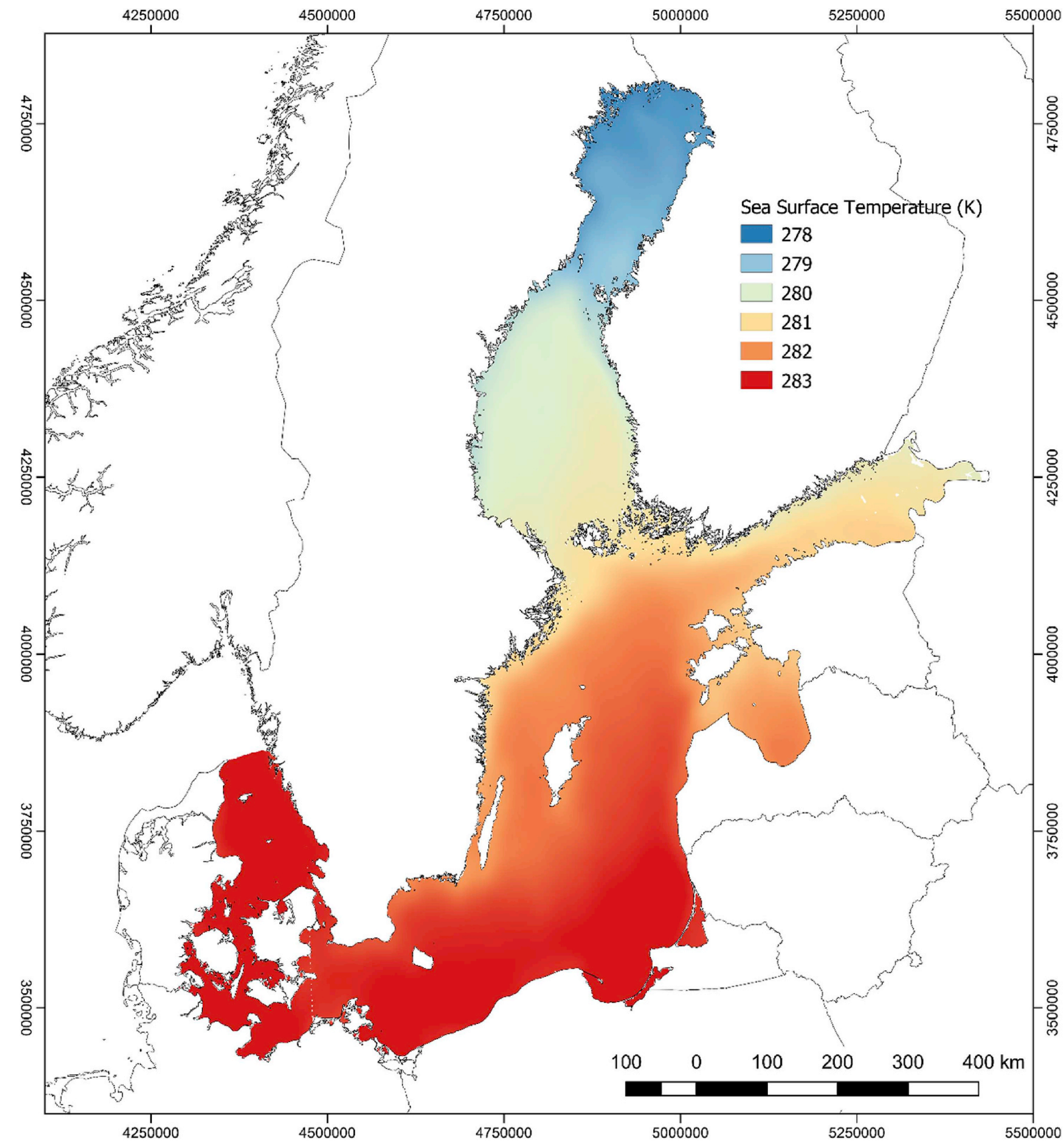
Sea depth in the Baltic Sea, from the Baltic Sea Hydrographic Commission.



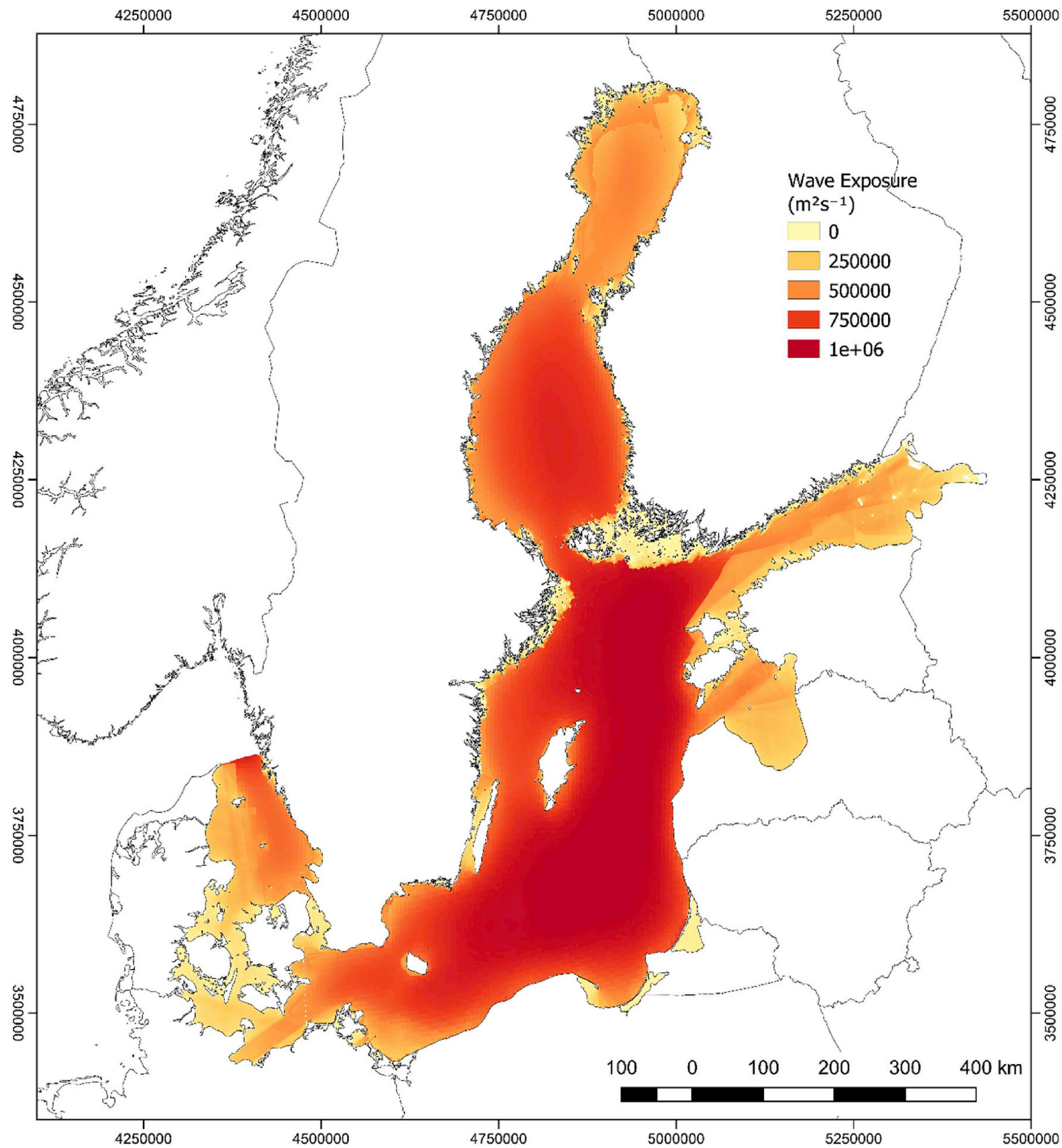
Modelled seabed sediment types in the Baltic Sea, from HELCOM, produced for the BALANCE project.



Shipping density in the Baltic Sea, from HELCOM.



Average sea surface temperature in the Baltic Sea, from the Danish Meteorological Institute.



Wave exposure in the Baltic Sea, from AquaBiota.

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