Predicted distributions of benthic flora and fauna in Polish waters

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Summary

To protect and manage the marine environment, maps of species and habitats are necessary. In the present study, GIS layers of the predictor variables depth, substrate (classified as mobile, non-mobile or anthropogenic), organic content of the surface sediment, wave exposure at the sea floor and sun-sea floor angle have been developed for the Polish Exclusive Economic Zone (EEZ). Through Generalised Additive Modelling (GAM), the influence of the predictor variables has been analysed on 30 species or taxonomic groups of benthic flora and fauna. The models have been used to create GIS layers of predicted distributions of all biota. Although the study is constrained by limited spatial distribution of samples of benthic biota and varying quality in the input data for some of the predictor variables, the overall results are ecologically sound and valuable for future studies of the benthic habitat in Polish waters.

Introduction

To protect and manage the marine environment, maps of species and habitats are necessary. Mapping the marine environment is recommended in e.g. HELCOM Recommendations 21/4 on protection of heavily endangered or immediately threatened marine and coastal biotopes in the Baltic Sea area, and 24/10 on implementation of integrated marine and coastal management of human activities in the Baltic Sea area. The present study is a carried out within the framework of the project “Ecosystem approach to marine spatial planning – Polish marine areas and the Natura 2000 network”. The overall aims of the project are to (1) rationalise the process of creating maps for planning of protected marine areas and (2) produce maps of ecosystem values of Polish marine habitats. As a part of the project, the present study has been carried out to produce maps of predicted distribution of benthic flora and fauna in Polish waters.

Materials and methods

Geographical areas

Biological data were available from five sampling areas in Polish waters; Slupsk Bank, the coastal area between Stilo and Utska, inner Puck Bay and two smaller areas in outer Puck Bay; Oksywie and Jurata. The sizes of the sampling areas are given in Table 1 and their positions are shown in Figure 1. The size of the entire Polish Exclusive Economic Zone (EEZ) is 32 539 km$^2$.

Table 1. Overview of the sampling areas; size and number of biological samples available.

<table>
<thead>
<tr>
<th>Area</th>
<th>Size (km$^2$)</th>
<th>Benthic flora samples</th>
<th>Benthic fauna samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slupsk Bank</td>
<td>118</td>
<td>108</td>
<td>106</td>
</tr>
<tr>
<td>Stilo-Utska</td>
<td>48</td>
<td>62</td>
<td>62</td>
</tr>
<tr>
<td>Inner Puck Bay</td>
<td>111</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td>Oksywie</td>
<td>3</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Jurata</td>
<td>1</td>
<td>15</td>
<td>13</td>
</tr>
<tr>
<td><strong>Sum</strong></td>
<td><strong>281</strong></td>
<td><strong>248</strong></td>
<td><strong>240</strong></td>
</tr>
</tbody>
</table>
Developing GIS layers of predictor variables

Physical data were available in different types of data sets, often with a higher resolution in the sampling areas. To obtain GIS layers with the best available data, the data sets for the Polish EEZ were combined with data sets for the sampling areas. For all predictor variables, grids with a spatial resolution of 25 m were created. The biological and physical data sets are described below.

Depth intervals were available in GIS layers. The interval range varied between areas; every 0.5 m in the Slupsk Bank area, every 1 m in the Inner Puck Bay, and every 5 m in the remaining Polish EEZ. For the Slupsk Bank area, data were available as polygons. For the Inner Puck Bay, data were available as a grid with 5 m resolution. For the Polish EEZ, half of the isobars (every 10 m starting at 0 m) were available as a grid with a resolution of 50 m, while the other half (every 10 m starting at 5 m) were available as polygons. To calculate a grid with continuous depth for the entire Polish EEZ with the most detailed data available, (1) all grids were converted to polygons, (2) evenly distributed points were added to all polygons, (3) depth values were added to all points, (4) when available, points from sampling areas replaced points from the EEZ layer, and (5) the final layer was calculated using the ArcGIS 9.3 Topo To Raster tool. The distance between the points on the polygons was chosen so that the smallest features of the isobars would be represented.

Surface sediment data were available as a grid with a resolution of 5 m for the Inner Puck Bay and as polygons for the other areas. The information was more detailed for all sampling areas than for the remaining Polish EEZ. In the Polish EEZ, natural sediments had been classified according to Shepard (1963), with an additional four sub-types of sand. In total, the granulometry of the Polish EEZ was described in 18 classes including anthropogenic sediments. Similar classes had been used for the
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Stilo-Utska area and the Inner Puck Bay. However, in the Slupsk Bank area, the habitat had been described in accordance with the EUNIS system at level two or three (EEA 2008). Four habitat classes had been used, three from the present EUNIS system and one new that was suggested to be included in the system. The proposed new class was called “mosaic of mobile and non-mobile substrates”. In order to use one classification system for all areas, all sediments were reclassified as mobile, non-mobile or anthropogenic. As both mobile and non-mobile substrate was present in the mosaic features, two alternative GIS layers were created; one in which the mosaic was classified as mobile substrate (“substrate A”) and one in which it was classified as non-mobile substrate (“substrate B”). To obtain the two alternative substrate grids for the entire Polish EEZ using data with the highest spatial resolution available, (1) all grids were converted to polygons, (2) less detailed data was replaced with more detailed data in areas where this was available, (3) features of the same substrate class were combined and (4) the polygons were converted to a grid.

Data on organic content of the surface sediment was available in 1350 unevenly distributed points throughout the Polish EEZ. A grid was interpolated using the spline method with the coastline as a barrier.

Wave exposure at the sea surface had been calculated for coastal Polish waters with a resolution of 25 m by Isæus et al. (2008) using the Simplified Wave Model method SWM (Isæus 2004). The available layer was extrapolated to include the offshore waters of the Polish EEZ.

Wave exposure at the sea floor was calculated based on the developed layers of wave exposure at the sea surface and depth, respectively, with a script developed by Bekkby et al. (2008).

The angle between the sun and the sea floor was derived from the slope and slope direction of the sea floor, both calculated from the developed layer of depth.

**Data on benthic flora and fauna**

Benthic flora and fauna had been collected with a systematic method developed within the Habitat Mapping project. In short, a three dimensional map of the seabed had been developed from side scan sonar and echo sound data. Based on this map, bottom habitats had been identified and delineated. Benthic flora and fauna had been collected at stations representing all habitat types where they were expected to be found (MIG 2007). The flora samples had exclusively been collected by scuba divers using a DAK device with a sample area of 400 cm$^2$ and a sampling depth of 5 cm. The DAK device is described in a project report (MIG 2007). Benthic fauna had primarily been sampled with the same technique, although a small portion (18 samples) were collected using a van Veen grab with a sample area of 1 120 cm$^2$. The number of samples that had been collected in each sampling area is shown in Table 1. All samples were analysed in the lab. For all samples, data on position, sampling method and occurring species or taxonomic groups were recorded.

<table>
<thead>
<tr>
<th>Data on benthic flora and fauna</th>
</tr>
</thead>
</table>

| Table 2. Ranges of the continuous predictor variables in the samples (“observed range”) and in the entire Polish EEZ (“predicted range”), respectively. |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| Depth (m)                       | Sun-sea floor angle | Organic content (%) | Wave exp. at sea surface (log scale) | Wave exp. at sea floor (log scale) |
| Observed range                  | 0.7 – 22.5         | -0.04 – 0.04      | 0 – 9.9         | 2.3 – 6.5         | 0.1 – 5.5         |
| Predicted range                 | 0 – 121            | -0.15 – 0.18      | 0 – 15          | 4.2 – 6           | -7 – 6            |
As the spatial distribution of the samples were restricted to relatively small areas within the Polish EEZ (Figure 1), the ranges of the continuous predictor variables in the samples and in the entire Polish EEZ are shown in Table 2.

**Analyses of correlations between predictor variables**

Pair-wise analyses were carried out to identify correlated variables that could not be used in the same model. The correlation between depth and wave exposure at sea surface was 0.85 and hence should not be used in the same model. As wave exposure at sea surface in general caused unrealistic response curves (see “Statistical modelling, model selection and spatial probability prediction” below), this variable was excluded from the statistical modelling. The correlations between depth and all other variables (substrate A and B, organic content and wave exposure at sea floor) were ±0.48 - ±0.69. The correlations between sun-sea floor angle and all other variables were ±0.01 - ±0.13. The correlations between organic content and the variables substrate A or B and wave exposure at sea floor were ±0.35 - ±0.53. The correlations between substrate A or B and wave exposure at sea floor was ±0.55 - ±0.64. All correlation values include comparisons for both benthic flora and benthic fauna samples.

**Statistical modelling, model selection and spatial probability prediction**

The effects of the predictor variables on the distribution of benthic flora and fauna was analysed by Generalised Additive Modelling (GAM) in the R 2.5.1 software (R Developmental Core Team 2007) with the extension GRASP (Lehmann et al. 2003). The response variable was presence/absence of biota and two degrees of freedom was set for the smoothing spline function.

As two alternative layers for substrate was available, substrate A (with mosaic features classified as mobile) was used for biota preferring mobile substrate, and substrate B (with mosaic features classified as non-mobile substrate) was used for biota preferring non-mobile substrate. An overview of the predictor variables in all models is shown in Table 3.

The response curves of the biota on all predictor variables were examined for unrealistic response due to e.g. uneven sampling distribution over the range of the variable. This revealed that the variable wave exposure at sea surface caused unrealistic response curves for all species. Further, the variable organic content caused unrealistic responses at high levels for 23 species or taxonomic groups and the variable depth did so for one species. In all cases an unrealistic response was found for a species or taxonomic group to a predictor variable, that variable was omitted from the statistical modelling for that species or taxonomic group.

In GRASP, the predicted probability model produced for each species or taxonomic group can be validated using an internal Receiver-Operating Characteristic (ROC) test and a cross-validated ROC (cvROC) test (Fielding and Bell 1997). The cvROC test evaluates the model against the dataset used for the modelling. A cvROC value of 1 indicates a perfect fit of the data to the model, while a value of 0.5 indicates a totally random response. Only models with a cvROC value above 0.75 were used to produce spatial predictions of biota.
Table 3. Overview of the statistical models for benthic (a) flora and (b) fauna. Org. cont. = organic content, substr. = substrate (classified as mobile or non-mobile), wave exp. = wave exposure at sea floor.

<table>
<thead>
<tr>
<th>(a) Flora</th>
<th>Possible predictor variables</th>
<th>Selected variables</th>
<th>ROC</th>
<th>cvROC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrochaetium sp.</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>sun-sea floor angle, substr.(^b), wave exp.</td>
<td>0.87</td>
<td>0.83</td>
</tr>
<tr>
<td>Ceramium spp.</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>0.90</td>
<td>0.86</td>
</tr>
<tr>
<td>Chaetomorpha linum</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, wave exp.</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Chara baltica</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, wave exp.</td>
<td>0.99</td>
<td>0.96</td>
</tr>
<tr>
<td>Cladophora glomerata</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, org. cont., wave exp.</td>
<td>0.98</td>
<td>0.94</td>
</tr>
<tr>
<td>Coccotylus truncatus</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b)</td>
<td>0.96</td>
<td>0.96</td>
</tr>
<tr>
<td>Delesseria sanguinea</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, substr.(^b)</td>
<td>0.87</td>
<td>0.82</td>
</tr>
<tr>
<td>Furcellaria lumbricalis</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>sun-sea floor angle, org. cont., substr.(^b)</td>
<td>0.99</td>
<td>0.98</td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle</td>
<td>0.96</td>
<td>0.95</td>
</tr>
<tr>
<td>Pilayella littoralis, Ectocarpus siliculosus</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>0.95</td>
<td>0.93</td>
</tr>
<tr>
<td>Polysiphonia fucoides</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>0.83</td>
<td>0.79</td>
</tr>
<tr>
<td>Potamogeton spp.</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, wave exp.</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Rhizoclonium implexum</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, substr.(^b), wave exp.</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Rhodomela confervoides</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, substr.(^b)</td>
<td>0.89</td>
<td>0.85</td>
</tr>
<tr>
<td>Zannichellia palustris</td>
<td>depth, sun-sea floor angle, substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle</td>
<td>0.92</td>
<td>0.91</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>depth, sun-sea floor angle, org. cont., substr.(^b), wave exp.</td>
<td>depth, sun-sea floor angle, wave exp.</td>
<td>0.95</td>
<td>0.90</td>
</tr>
</tbody>
</table>
### (b) Fauna

<table>
<thead>
<tr>
<th>Fauna</th>
<th>Possible predictor variables</th>
<th>Selected variables</th>
<th>ROC</th>
<th>cvROC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathyporeia pilosa</td>
<td>sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>sun-sea floor angle, substr., wave exp.</td>
<td>0.95</td>
<td>0.92</td>
</tr>
<tr>
<td>Cerastoderma glaucum</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>sun-sea floor angle, substr., wave exp.</td>
<td>0.98</td>
<td>0.96</td>
</tr>
<tr>
<td>Cyathura carinata</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>depth, sun-sea floor angle, wave exp.</td>
<td>0.97</td>
<td>0.88</td>
</tr>
<tr>
<td>Fabricia sabella</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>depth, org. cont., substr.</td>
<td>0.86</td>
<td>0.85</td>
</tr>
<tr>
<td>Gammarus spp.</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>depth, substr., wave exp.</td>
<td>0.89</td>
<td>0.86</td>
</tr>
<tr>
<td>Idotea chelipes</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>0.82</td>
<td>0.62</td>
</tr>
<tr>
<td>Jaera sp.</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>depth, org. cont., substr.</td>
<td>0.97</td>
<td>0.94</td>
</tr>
<tr>
<td>Macoma balthica</td>
<td>depht, sun-sea floor angle, substr., wave exp.</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>0.87</td>
<td>0.83</td>
</tr>
<tr>
<td>Melita palmata</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>sun-sea floor angle, org. cont., wave exp.</td>
<td>0.94</td>
<td>0.92</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>depth, org. cont., substr.</td>
<td>0.90</td>
<td>0.86</td>
</tr>
<tr>
<td>Mytilus trossulus</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>sun-sea floor angle, substr., wave exp.</td>
<td>0.89</td>
<td>0.87</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>depth, sun-sea floor angle</td>
<td>0.79</td>
<td>0.78</td>
</tr>
<tr>
<td>Praunus flexuosus</td>
<td>depth, sun-sea floor angle, org. cont., substr., wave exp.</td>
<td>org. cont., substr., wave exp.</td>
<td>0.85</td>
<td>0.82</td>
</tr>
<tr>
<td>Theodoxus fluviatilis</td>
<td>depth, sun-sea floor angle, substr., wave exp.</td>
<td>depth, substr., wave exp.</td>
<td>0.84</td>
<td>0.80</td>
</tr>
</tbody>
</table>

* A: Mosaic features in the original layer classified as mobile substrate.
* B: Mosaic features in the original layer classified as non-mobile substrate.

In GRASP, the response curves of the GAM are used to produce a matrix of predictions within defined ranges. These ranges were set to the maximum and minimum values of the predictor variable within the Polish EEZ. In ArcView 3.3, grids of predicted distribution of biota were produced based on the matrix and grids of the predictor variables. The grids of predicted distribution of biota were produced with the same spatial resolution as the predictor variables, i.e. 25 m.

As extrapolations were made into deeper waters than sampled, all results were investigated for positive correlations between the occurrence of biota and depth at the depth of 22.5 m. If a species
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was predicted to reach its maximum occurrence at the maximum depth and this was considered unlikely, the prediction was cut at either the deepest known occurrence or at 22.5 m.

**Results**

Maps of the predictor variables used in the modelling of benthic biota in the Polish EEZ are shown in the following figures; water depth (Figure 2), mobile, non-mobile and anthropogenic substrate (Figure 3), organic content of the surface sediment (Figure 4) wave exposure at the sea floor (Figure 5) and sun-sea floor angle (Figure 6).

![Figure 2. Depth in the Polish EEZ.](image-url)
Figure 3. Substrate in the Polish EEZ. Features described as mosaic of mobile and non-mobile substrata in the original layer are classified as (a) mobile substrate and (b) non-mobile substrate, respectively.
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Figure 4. Organic content of surface sediment in the Polish EEZ.

Figure 5. Wave exposure at the sea floor in the Polish EEZ.
Maps of predicted distributions of benthic flora are shown in Figures 7-22 and of fauna in Figures 23-36. Note that the scales of probability of occurrence differ between the maps and that the spatial distributions of *Delesseria sanguinea*, *Cerastoderma glaucum*, *Macoma balthica* and *Mya arenaria* have been cut a certain depths. The selected predictor variables, ROC values and cvROC values of all models are shown in Table 3.
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Figure 7. Predicted distribution of *Acrochaetium* sp. in the Polish EEZ.

Figure 8. Predicted distribution of *Ceramium* spp. in the Polish EEZ.
Figure 9. Predicted distribution of *Chaetomorpha linum* in the Polish EEZ.

Figure 10. Predicted distribution of *Chara baltica* in the Polish EEZ.
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Figure 11. Predicted distribution of *Cladophora glomerata* in the Polish EEZ.

Figure 12. Predicted distribution of *Coccotylus truncatus* in the Polish EEZ.
Figure 13. Predicted distribution of *Delesseria sanguinea* in the Polish EEZ. The prediction has been cut at a depth of 30 m.

Figure 14. Predicted distribution of *Furcellaria lumbricalis* in the Polish EEZ.
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Figure 15. Predicted distribution of *Myriophyllum spicatum* in the Polish EEZ.

Figure 16. Predicted distribution of *Pilayella littoralis* and *Ectocarpus siliculosus* in the Polish EEZ.
Figure 17. Predicted distribution of *Polysiphonia fucoides* in the Polish EEZ.

Figure 18. Predicted distribution of *Potamogeton* spp in the Polish EEZ.
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Figure 19. Predicted distribution of *Rhizoclonium implexum* in the Polish EEZ.

Figure 20. Predicted distribution of *Rhodomela confervoides* in the Polish EEZ.
Figure 21. Predicted distribution of *Zannichellia palustris* in the Polish EEZ.

Figure 22. Predicted distribution of *Zostera marina* in the Polish EEZ.
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Figure 23. Predicted distribution of *Bathyporeia pilosa* in the Polish EEZ.

Figure 24. Predicted distribution of *Cerastoderma glaucum* in the Polish EEZ. The prediction has been cut at a depth of 22.5 m.
Figure 25. Predicted distribution of *Cyathura carinata* in the Polish EEZ.

Figure 26. Predicted distribution of *Fabricia sabella* in the Polish EEZ.
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Figure 27. Predicted distribution of *Gammarus* spp. in the Polish EEZ.

Figure 28. Predicted distribution of *Idotea chelipes* in the Polish EEZ.
Figure 29. Predicted distribution of *Jaera* sp. in the Polish EEZ.

Figure 30. Predicted distribution of *Macoma balthica* in the Polish EEZ. The prediction has been cut at a depth of 22.5 m.
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Figure 31. Predicted distribution of *Melita palmata* in the Polish EEZ.

Figure 32. Predicted distribution of *Mya arenaria* in the Polish EEZ. The prediction has been cut at a depth of 22.5 m.
Figure 33. Predicted distribution of *Mytilus trossulus* in the Polish EEZ. The prediction has been cut at a depth of 80 m.

Figure 34. Predicted distribution of *Oligochaeta* in the Polish EEZ.
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Figure 35. Predicted distribution of *Praunus flexuosus* in the Polish EEZ.

Figure 36. Predicted distribution of *Theodoxus fluviatilis* in the Polish EEZ.
Discussion

Layers of predictor variables and their effects on the predicted distributions of biota

The depth layer was calculated with the ArcGIS 9.3 Topo To Raster tool, which is developed for interpolation of a hydrologically correct surface from various types of input data. This means that the tool may not be optimal for a marine environment. In the developed depth layer several ridges can be seen, e.g. perpendicular from the coastline. These are most likely artefacts from the interpolation method and not true underwater ridges. Effects of these questionable ridges can be distinguished in the predicted distribution of *Mya arenaria*, primarily in shallow waters. The ridges can be seen in the maps of predicted distribution of several other species as well, but for all other species, the ridges are or may also be caused by the layer of sun-sea floor angle (see below).

The substrate layers contain very few features as only three universal classes could be created from the original data. Nevertheless, the information was shown to be useful as the variable was selected for the majority of the models. The non-mobile substrate features can be clearly seen in the predicted distribution of e.g. most species of red algae, *Theodoxus fluviatilis* and *Idotea chelipes*. By choosing the layer with the entire feature “mosaic of mobile and non-mobile substrates” classified as the preferred substrate for the modelled species, the entire feature is considered as potential habitat although parts of it is not. This was preferred in favour of (1) using the layer with the non-preferred habitat class, despite that preferred habitat was present, and (2) excluding the feature completely from the analyses.

The layer of organic content was interpolated from data points with varying spatial distribution and several cases of samples with very different values next to each other. This resulted in an uneven layer; areas with low sample density are generally uniform while areas with higher sample density are highly variable. Throughout the layer, single samples that differ substantially from the neighbouring samples can be distinguished. In the map of the predicted distribution of *Cladophora glomerata*, the algae is absent in the areas with high organic content in Puck Bay, despite that the other environmental parameters in the model (depth, sun-sea floor angle and wave exposure) are favourable for the species. The predicted distribution of *Melita palmata* is concentrated to the areas with slightly higher organic content (1-2%) than the surroundings along the Polish coast.

Due to the uniform shape of the Polish coastline, the layer for wave exposure at the sea floor is generally uniform with lower exposure in deep waters and higher exposure in shallow waters. Low exposure close to the shore can only be found in Puck Bay. The importance of wave exposure can be seen in the predicted distributions of *Idotea chelipes* that is calculated to occur in sheltered waters primarily shallower than 20 m. All modelled species of green algae and vascular plants were found to prefer the shallow and sheltered waters in Inner Puck Bay.

The layer of sun-sea floor angle is calculated from the depth layer (see Materials and methods). The questionable ridges in the depth layer are even more pronounced in the layer of sun-sea floor angle. These ridges are also found in the very similar predicted distributions of *Coccolytus truncates* and *Furcellaria lumbricalis*. For both of these species, sun-sea floor angle but not depth was selected as a predictor variable in the models. In shallow waters, the ridges can also be seen in the predicted
distribution of *Cerastoderma glaucum*. The layer of sun-sea floor angle was selected as a predictor variable in 88% of the models for benthic flora, but only in 50% of the models for benthic fauna. For some of the fauna species, the selection of the variable sun-sea floor angle may reflect that its distribution is correlated to that of benthic flora.

**Effects of limited sampling range**

As the spatial distribution of samples was restricted to the sampling areas, the predictions had to be extrapolated to cover the entire Polish EEZ. As shown in Table 2, the deepest sample was taken at 22.5 m depth, while the deepest part of the Polish EEZ is 121 m. This is also mirrored in the wave exposure data. While the samples represent the extent of the wave exposure at the sea surface fairly well, the sheltered water at the sea floor in deep areas is not represented. For the variable sun-sea floor angle, only intermediate values are sampled in comparison to the range in the entire Polish EEZ. For the variable organic content, the samples represent the total range fairly well. In summary, extrapolations have mainly been made for waters deeper than 22.5 meters and for areas with steep slopes.

If a species distribution continues beyond the sampled range, only a part of the species response curve to the predictor variable will be known. Three common problems with this are; (1) if only the lower part of a true monomodal response is observed, the response is interpreted as a positive or negative correlation, (2) if the response reaches its vertex close to the maximum value of the sampling range, only a few observations may be needed below the vertex to change the response curve and hence all extrapolations, and (3) if little response is found within the sampled range of the variable, the predictor variable may not be selected for the model although it is of importance within the range of the prediction. The first problem was demonstrated in the response curves of *Delesseria sanguinea* that showed a positive correlation between depth and occurrence throughout the sampling range. As the species is usually not found below 30 m in the Baltic Sea (Wærn 1976), the prediction was cut at this depth. In the resulting map (Figure 13), the pattern of increasing probability of presence down to 30 m is questionable. The true probability of presence may reach its maximum at a shallower depth and thereafter decrease with increasing depth, although that maximum may be close to 30 m. The second problem was found for the mussels *Macoma balthica* and *Mya arenaria*. The species showed a negative response to depth down to approximately 15 m, where it turned to a positive response due to 2-3 records of presence and 2-3 records of absence below 20 m. To avoid extrapolation of this error, the predicted distributions of *Mya arenaria* and *Macoma balthica* were cut at maximum sampling depth, i.e. 22.5 m. The third problem was observed in the models of the mussels *Cerastoderma glaucum* and *Mytilus trossulus*. Consequently the distribution of *Cerastoderma glaucum* was cut at 22.5 m. However, as *Mytilus trossulus* is known to occur in waters to 80 m depth in Polish waters (Weslawski pers. comm.), this prediction was cut at 80 m.

As no independent validation data set has been available for the study, the maps of predicted distributions should be interpreted with caution. Nevertheless, the spatial predictions of biota are in general ecologically sound. They are useful in studies of potential distribution of benthic species and habitats in Polish waters and can be evaluated with independent data in the future.
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References


