Mapping an ecosystem service: A quantitative approach to derive fish feeding ground maps*

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Abstract

This study presents a quantitative approach to mapping benthophagous fish feeding grounds. This approach combines the spatial biomass distribution of benthic prey items and their importance for the diets of predators. A point based biomass data of macrozoobenthos together with a set of environmental factors was used

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to develop Random Forests models that produce continuous biomass distribution layers for individual prey species. Depending on the diet composition and the importance of prey for fish feeding, these layers are overlaid and an integrated GIS map of the seabed showing the quality of feeding grounds is generated. These maps provide a useful basis for conservation and marine spatial planning. In addition, this method could be applied to the mapping of resources used by other benthophagous organisms. The method is presented using the example of three common Baltic fish species: cod, flounder and viviparous eelpout.

1. Introduction

Studies of ecosystem goods and services in marine environments are receiving increasing attention (Kremen & Ostfeld 2005, Ronnback et al. 2007). Whereas concepts are rapidly developed, quantitative approaches or assessments are rare; furthermore, many of them focus on mapping service values (Troy & Wilson 2006, Sanchirico & Mumby 2009), not the services themselves. One of the most important ecosystem services provided by the seafloor is the feeding grounds for many benthophagous organisms such as fish or marine birds. Moreover, apart from other roles in ecosystem processes (Snelgrove 1998), benthic macrofauna is also an important food source for higher trophic levels in aquatic ecosystems (Tomczak et al. 2009). There are ca 200 macrozoobenthos species in the eastern Baltic Proper (Ojaveer et al. 2010), although only a few of them are known to be important in the diet of benthivorous fish (Järvekülg 1979). Nevertheless, large Baltic fish species such as cod, flounder or eelpout, apart from small fish and nectobenthic species, feed intensively on a wide spectrum of benthic invertebrates such as isopods *Saduria entomon*, bivalves *Macoma balthica, Mytilus edulis, Mya arenaria* and even relatively small polychaete worms and amphipods (Mulicki 1947, Urtans 1992, Ostrowski 1997, Didžiulis 1999, Bubinas & Ložys 2000, Uzars 2000). Owing to the various environmental demands of benthic species, feeding conditions for specific fish species are supported to a specific degree by different habitats. Moreover, since the abundance and biomass of macrofauna vary significantly within a habitat (Thrush et al. 1994), a habitat map alone is not sufficient, as the value of a feeding ground service varies at a scale smaller than that of the habitat. On the other hand, there are plenty of papers on the distribution and abundance of macrofauna (Ellis et al. 2006, Potts & Elith 2006, Willems et al. 2008, Gogina & Zettler 2010), especially since the significant increase in different modelling techniques in benthic ecology studies (Collin et al. 2011, Reiss et al. 2011). However, studies on the prediction of biomass are rare, despite its applications in fisheries (Wei et al. 2010).

In this study we suggest an approach for making a quantitative assessment of one specific benthic habitat service, namely fish feeding grounds, based on the diet of fish and the modelling of prey biomass. We present the method using the example of three common Baltic fish species: Baltic cod (*Gadus morhua* Linnaeus, 1758), flounder (*Platichthys flesus* Linnaeus, 1758) and viviparous eelpout (*Zoarces viviparus* Linnaeus, 1758). The output of the assessment is a fish feeding ground service map where the seabed is classified by its quality for foraging fish.

2. Material and methods

2.1. General scheme of the assessment

The assessment procedure includes three parts: modelling of macrozoobenthos biomass (service provider module), analysis of fish prey items (service user module) and the output of the assessment: the quality map of fish feeding ground service (Figure 1). The first step is data acquisition: fish and macrofauna samples are gathered and processed, and then GIS layers of environmental factors (predictors) are created. The diets of the separate fish species are identified from an analysis of fish digestive tracts, after which biomass distribution models of prey items are set up on the basis of macrofauna sample analysis and layers of environmental predictors.

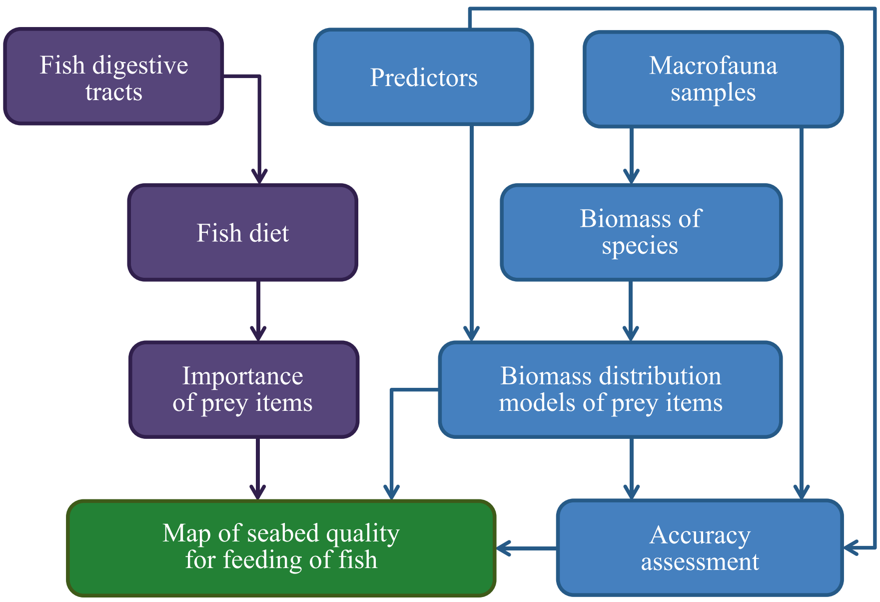

Figure 1. General scheme of the assessment procedure for mapping fish feeding ground service. Blue – service provider module, purple – service user module, green – output of the approach

In the next step, weights for prey items are assigned, depending on their importance to the diet of a particular fish species, and in parallel, model predictions are transferred into the GIS environment, where biomass distribution maps are developed. Finally, biomass maps of separate prey items with assigned weights are overlaid and maps of fish feeding grounds are generated. In addition, the accuracy is assessed to identify the reliability of the maps. The data in the service user module are not directly related to the service provider module and can be modified in accordance with the aims of the study (i.e. feeding grounds of a single fish species).

2.2. Study area & environmental predictors

This study was carried in the Lithuanian Exclusive Economic Zone (ICES subdivision 26), south-eastern Baltic Sea. Of the available environmental predictors known to be important for the distribution of macrozoobenthos (Olenin 1997, Bučas et al. 2009, Gogina & Zettler 2010, Reiss et al. 2011), eight were selected for the modelling of prey biomass: salinity, minimum near-bottom oxygen concentration, near-bottom current velocity, wave generated orbital near-bottom velocity, depth, sediment types, areas with the presence or absence of the thermocline and the areas above and below the halocline. Quantitative environmental parameters were tested for collinearity and predictors were removed from models if variance inflation factors (VIF) were > 3 (Quinn & Keough 2002). Depth was highly collinear with the wave-generated near-bottom orbital velocity, near-bottom oxygen concentration and salinity. These three predictors are direct environmental factors for the distribution of macrofauna, whereas depth is a cumulative and indirect effect of them (McArthur et al. 2010) and was therefore omitted. The layer of sediments was derived from geological charts (Repečka et al. 1997, Gelumbauskaitė et al. 1999, Bitinas et al. 2004). Sediments were classified into four types: boulders, cobbles/gravel, sand and silt (Wentworth 1922). The wind wave orbital velocity data layer was derived using the SWAN model (Booij et al. 1999) based on 2008–2009 wind data. National marine monitoring data was used to derive the salinity and thermocline/halocline layers (MRC, unpublished: 2003–2008 and 1998–2006 datasets accordingly). Minimum near-bottom oxygen concentrations (2000–2006) and annual mean bottom current velocity layers were obtained from datasets produced by the BALANCE project (Hansen et al. 2007, Bendtsen et al. 2007).

2.3. Field data

Data on the feeding habits of Baltic cod, flounder and viviparous eelpout of different body length were collected in the spring-autumn seasons of

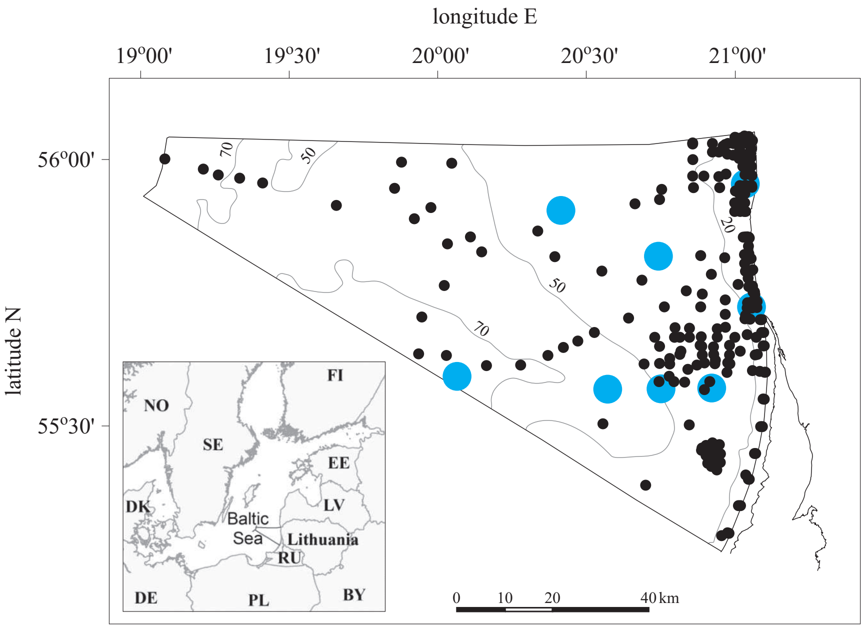

Figure 2. Exclusive Lithuanian economic zone with field stations where samples of macrozoobenthos (black dots) and fish samples (blue dots) were taken for the present study during 1998–2010. Grey lines indicate the 20, 50 and 70 m isobaths

2000–2010 during quarterly trawl surveys. Stomach contents were analysed by standard numerical and gravimetric methods (Hyslop 1980). To assess the diet composition of fish 1425 digestive tracts were analysed (empty tracts excluded): 300 digestive tracts of Atlantic cod (from 39 to 80 cm in size); 1000 digestive tracts of flounder (the size ranged from 15 to 40 cm); 125 digestive tracts of eelpout (sizes from 25 to 30 cm). Food items were identified to the lowest possible taxonomic level. In total, data from 640 benthic samples taken at 224 sampling sites during 1998–2010 were used to model the biomass distribution of the macrozoobenthos (Figure 2). Soft-bottom samples were taken with a Van Veen grab, while hard bottoms were sampled by SCUBA divers with a 0.20 × 0.20 m frame. Samples were taken and treated following standard guidelines for bottom macrofauna sampling (HELCOM 1988).

2.4. Occurrence and importance of prey items

The occurrence and importance of prey items were inferred from the analysis of fish digestive tracts. The former describes the relative frequency of a particular prey in all digestive tracts, while the latter indicates how much a particular prey item contributes to the total content in a discrete

Table 1. Occurrence in digestive tracts (first letter) and importance (second letter) of prey items for cod, flounder and eelpout. Empty cells indicate that fish do not prey on that particular item. H – high, M – moderate, L – low

Prey items	Occurrence/Importance		
	Cod	Flounder	Eelpout
Gammaridea	H/H	H/H	H/M
Halicryptus spinulosus		M/M	
Hediste diversicolor	M/L	M/L	M/L
Macoma balthica		H/H	M/M
Marenzelleria neglecta	L/L	L/L	L/L
Mya arenaria		L/L	
Mytilus edulis		M/M	L/L
Saduria entomon	H/H	M/L	M/L

digestive tract. Both parameters were divided into three categories: high, moderate and low. A '*high*' occurrence means that a particular benthic animal is found in more than 50% of samples, '*moderate*' – in 20–50% of samples and '*low*' in < 20% of samples. A '*high*' importance means that most of the digestive tract can be filled with a particular prey species (more than 50% of tract content), '*moderate*' – 20–50% of tract content, while'*low*' means that a particular item is only a small addition to the whole tract content (< 20% of tract content). The occurrence and importance of prey items are shown in Table 1. As the study aimed to evaluate the quality of the seabed for the feeding of fish, the assessment was based only on benthic invertebrates, excluding nectobenthic species and small pelagic fish.

2.5. Spatial distribution of prey item biomass

To predict the biomass distribution of prey species the Random forests (RF) regression model (Breiman 2001) implemented in the 'randomForest 4.6-2' package (Liaw & Wiener 2002) within the R environment was chosen.

The modelling procedure was as follows. First of all, a correlation matrix was created for all predictors. If a correlation coefficient was > 0.7 or the VIF (variance inflation factors) were > 3, those predictors were not used for constructing the model. Then the biomass data were split into two sets: train data (70% of all data) for constructing the model and test data (the remaining 30%) for validation. In order to avoid an uneven distribution of zero values the split was made semi-randomly: all sites were chosen randomly but with the proviso that sites with zero values would distribute 70/30 in train/test datasets. Parameters for RF were selected as follows: the number of trees (ntree) was set to 1000, while the number of variables randomly selected at each node (mtry) and minimum node size (ndsize) were set to default values 2.3 and 5 respectively. After running the model the importance of the predictors was assessed. The Mean Decrease Accuracy (%IncMSE) was calculated to assess the importance of every environmental factor for the response variable. During validation, predicted values were compared with observations of external data (test dataset), thereby revealing the model's true performance. Several estimates were calculated: (1) MAD – mean absolute deviation, (2) $\mathrm{CV_{MAD}}$ – coefficient of variation of MAD, $\mathrm{r_s}$ – Spearman's correlation between observed (y_t) and predicted ($\widehat{y}_t$) values.

$$\mathrm{MAD} = n^{-1} \sum_{t=1}^{n} |y_t - \widehat{y}_t| \,, \tag{1}$$

$$\mathrm{CV_{MAD}} = \frac{\mathrm{MAD}}{\bar{y}} \times 100. \tag{2}$$

Finally, the data were exported to the GIS environment. Predictions were made for the whole research area in a 100 × 100 m grid and together with coordinates were transcribed to a DBF file, which can be easily used with most GIS software.

2.6. Development of maps

The output file of a model was imported in ArcGIS 9.3.1 software. Using 'Natural Neighbour' interpolation, raster files of biomass distribution were produced. Rasters of those prey items that a particular fish species feeds on were added up with different weights (Table 2). Weights are given according to the *occurrence* and *importance* shown in Table 1. Initial biomass values were multiplied by the weight in order to better reflect the important feeding items in the feeding ground map. As different multipliers were used, biomass units were no longer suitable, so scores of weighted biomass was categorized into five levels of quality: *very high*, *high*, *moderate*, *low* and *very low*, where *very high* quality indicates the highest biomass aggregations of prey

Table 2. Raster weights according to the occurrence and importance of prey items for fish feeding. H – high, M – moderate, L – low

Occurrence/Importance	Weight
H/H	1
H/M or M/H	0.75
M/M	0.5
M/L or L/M	0.37
L/L	0.25

items with respect to their importance to fish diets. Finally, the maps for different fish species were combined and the map of overall seabed quality for the feeding of a given fish was produced.

2.7. Accuracy assessment

Three levels of accuracy were generated for the quality map of fish feeding grounds. The accuracy indicated how well or badly different quartiles of a predictor range were covered by macrofauna samples. First of all, the accuracy of biomass distribution of each prey item was estimated. In relation to partial plots, every predictor was split into four intervals/categories (predictors with presence/absence data were split into two) and the number of macrofauna samples was counted for each interval/category. Since 171 samples were used for the model build up, 171 was the total point pool split between intervals/categories of a single predictor. Then the 'Reclassify' function was used to reclassify the predictor layer assigning these points for all intervals/categories. These point scores were multiplied by the mean decrease accuracy value (Table 5) produced by the model. In this way the accuracy of the most important predictor receives the highest weight and minor predictors had a proportionally lower impact on overall accuracy. Finally, the accuracy layers of every prey item were added up, then split into three categories (high, moderate, low) using the geometrical interval classification method; ultimately, an accuracy layer for the feeding grounds was produced.

A '*high*' accuracy is interpreted as the best possible area modelled with the current dataset, though validation errors must still be taken into account. Areas of '*moderate*' accuracy should be treated as trustworthy, although they should be studied more closely before decision making. A '*low*' accuracy indicates areas that are modelled on the basis of just a few samples and should be treated with caution.

3. Diet composition of cod, flounder and eelpout

Eight macrozoobenthos species or higher taxa were identified during the analysis of fish stomach contents (Table 1). Cod mainly preyed upon isopods *Saduria entomon* and gammarideans, while polychaete worms were of minor importance. Preferred prey items for flounder and eelpout were gammarideans and bivalves *Macoma balthica*, while priapulids *Halicryptus spinulosus* and soft-shell clams *Mya arenaria* were eaten only by flounder. Flounder had the most diverse diet composition (a total of eight prey items), while eelpout and cod preyed upon six and four prey items respectively. Half of the prey items were eaten by all three species, while two items (*H. spinulosus* and *M. arenaria*) were exclusively fed on by flounder.

Table 3. Weight multipliers of prey items assigned according to occurrence and importance. Empty cells indicate that fish do not prey upon that particular item

Prey items	Cod	Flounder	Eelpout
Gammaridea	1	1	0.75
Halicryptus spinulosus		0.5	
Hediste diversicolor	0.37	0.37	0.37
Macoma balthica		1	0.5
Marenzelleria neglecta	0.25	0.25	0.25
Mya arenaria		0.25	
Mytilus edulis		0.5	0.25
Saduria entomon	1	0.37	0.37

Different weights were assigned to every fish species separately according to the *occurrence* and *importance* of prey items (Table 3).

3.1. Model performance

According to the coefficient of variation of mean absolute deviation (Table 4) the most accurate model was obtained for blue mussel *M. edulis* (16%). Models of *S. entomon*, Gammaridea, *H. spinulosus* and *M. arenaria* were also relatively accurate (< 50%). The model of *M. balthica* was less accurate (61%), and the accuracy was the lowest for both polychaete models (> 70%).

Table 4. Validation results of prey item biomass models. Columns from left to right: prey items; average sample biomass ± standard deviation; mean absolute deviation (MAD); coefficient of variation of MAD (CV_{MAD}); Spearman's correlation of observations and predictions

Prey items	Mean biomass [g m^{-2}]	MAD [g m^{-2}]	Validation CV_{MAD} [%]	r_s
Gammaridea	7.8 ± 16.3	2.6	33.2	0.48
Hediste diversicolor	2.0±3.2	1.4	71.2	0.57
Halicryptus spinulosus	0.3±1.1	0.1	38.1	0.46
Mya arenaria	6.5±17.4	3.0	46.3	0.41
Macoma balthica	43.4± 53.8	26.4	60.9	0.77
Mytilus edulis	1385.4±1398.9	223.5	16.1	0.62
Marenzelleria neglecta	3.8±9.4	2.7	70.1	0.34
Saduria entomon	5.6±5.8	1.8	32.6	0.76

The mean decrease accuracy (%IncMSE) was calculated for each predictor in order to evaluate its importance to the response variable (Table 5). The most important predictor was near-bottom oxygen concentration

Table 5. Mean decrease accuracy (%IncMSE) of environmental predictors. A higher value indicates greater importance. H.s. – *Halicryptus spinulosus*, Gam. – Gammaridea, M.n. – *Marenzelleria neglecta*, H.d. – *Hediste diversicolor*, M.e. – *Mytilus edulis*, M.a. – *Mya arenaria*, M.b. – *Macoma balthica*, S.e. – *Saduria entomon*

Predictors	Gam.	H.d.	H.s.	M.a.	M.b.	M.e.	M.n.	S.e.
current velocity	3.8	6.4	3.5	7.6	22.4	3.9	0.5	7.2
orbital velocity	2.4	12.0	12.7	6.9	18.0	9.6	7.9	18.9
salinity	6.7	16.3	3.8	0.2	25.1	17.0	7.4	15.0
oxygen concentration	7.1	10.7	12.1	9.2	28.7	16.1	3.9	24.6
sediment types	9.3	3.8	7.7	0.7	22.2	34.8	4.7	10.1
halocline	0.4	3.2	5.5	4.6	−1.4	1.4	1.3	6.3
thermocline	1.8	2.7	0.4	−4.2	14.4	10.4	0.7	5.8

especially for deep-living species like *M. balthica, S. entomon* and *H. spinulosus* (28.7, 12.1 and 24.6 %IncMSE respectively). Orbital velocity, salinity and sediments were also important: the biomasses of amphipods *M. edulis* were mostly dependent on sediments (9.3 and 34.8 %IncMSE respectively), while salinity had a major influence on both polychaete worms and *M. balthica*, and orbital velocity on *H. spinulosus* and *S. entomon* (12.7 and 18.9 respectively). Near-bottom current velocity was less important, while the halocline and thermocline were only of minor importance or of no importance at all in some cases.

3.2. Quality map of fish feeding grounds

The map of seabed quality for the feeding of cod, flounder and eelpout is presented in Figure 3.

The highest quality feeding grounds for all three fish species is the stony bottom in the coastal area situated in the northernmost part of LEZ. Other high quality areas are located in the offshore zone: one in an offshore bank with heterogeneous sediments at 50 m depth (western part of LEZ), another in the soft bottom at 40–50 m depths (central part of LEZ). The accuracy assessment indicates that the most accurate areas of the approach are at 10–40 m depths. The low accuracy areas were justified by only 18% of total samples and were set in very shallow areas (down to 3 m depth) and for the deepest areas. Accuracy was moderate for offshore areas in the central part of LEZ and for the coastal area. More than half the samples were taken in the coastal area, but because of the rapid changes in some environmental parameters (especially salinity and near-bottom orbital velocity) the quartiles of these predictors were only moderately justified in terms of accuracy.

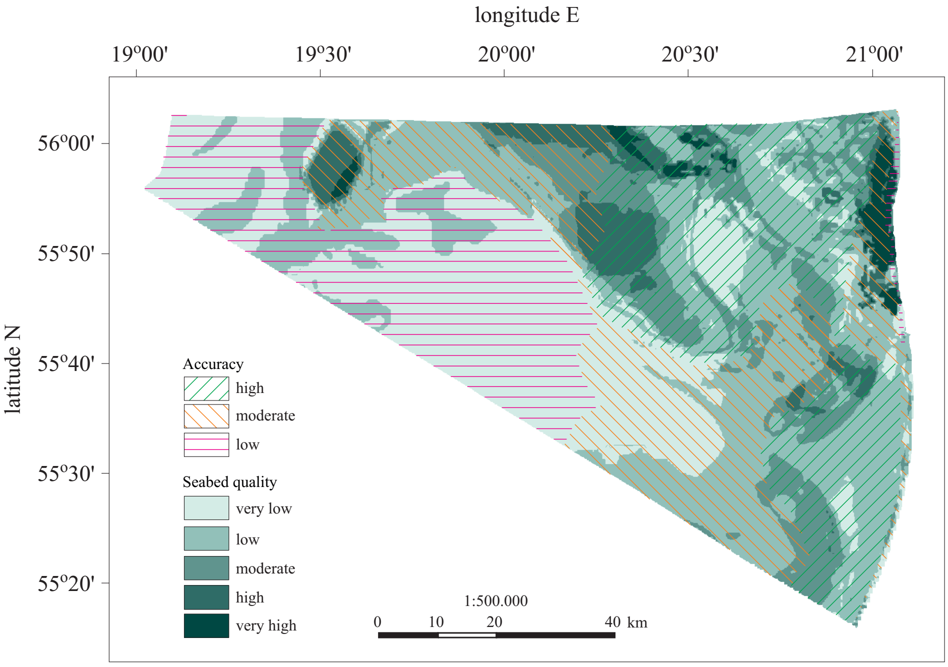

Figure 3. Map of seabed quality in the Lithuanian Economic Zone for the feeding of cod, flounder and eelpout (with an accuracy assessment)

4. Discussion

The proposed approach allows a map of the fish feeding ground service provided by the seabed to be constructed. Such maps provide a different view of the spatial distribution of valuable seabed areas as they do not necessarily coincide with the high catch areas of selected fish species. It is known that it can take more than 30 hours for prey to be digested (Macdonald et al. 1982), depending on the size of both predator and prey (Santos & Jobling 1991, Bromley 1994) as well as on water temperature (Tyler 1970). Furthermore, the sustained speed of cod can reach 0.6–0.9 BL s^{-1} (He 1991, Björnsson 1993), meaning that 60 cm cod can swim for 38–58 km before their prey are digested. This shows that high catch areas of mobile fish whose stomachs are filled with benthic invertebrates do not necessary correspond to the good quality of the seabed, for there is no proof that the fish were caught in an actual feeding ground. Certainly, this is not the case with low mobility species like flounder and eelpout. On the other hand, these maps do not evaluate the suitability of a given environment for fish species apart from the biomass distribution of prey items and their importance to the diet. It may happen that a prey biomass is very high but the fish has limited access to this environment or the environment may be unsuitable in the context of factors other than feeding. For instance, the eelpout is exclusively associated with coastal hard bottoms, so other areas (even of the highest quality) are irrelevant to this species. Nevertheless, if the quality map of feeding grounds were combined with fish distribution maps, it would elevate our knowledge to a different level.

As in many other modelling approaches the outcome of our method is dependent on the quality of the initial data. The type of data for the service user module can be selected according to the aim of a study (in our case relatively robust data were sufficient) and could range from several categories of importance based on expert knowledge to exact figures of prey numbers and their weight. For the service provider module of the best available data on both macrozoobenthos and predictors it would be advisable, for instance, to add other environmental parameters such as organic content and nutrient supply, which could obviously enhance the quality and applicability of models (Gogina & Zettler 2010). Furthermore, accuracy assessments have stressed that the different quartiles of a predictor range may be unevenly justified by macrofauna data, so the sampling strategy should take into account the spatial peculiarities of important predictors, especially that part of a range where significant changes in the characteristics of macrofauna occur.

Our method may have many other applications. The data in the user module (in this case the feeding of cod, flounder and eelpout) could easily be replaced by different objects like the feeding of other fish species or even birds. On the other hand, it could serve not only to map feeding grounds, but also other types of services or assessments, for instance, biological valorization, as suggested by Węsławski et al. (2009) or habitat sensitivity, as implemented by Hiscock & Tyler-Walters (2006). Finally, if biomass data were replaced with abundance of macrozoobenthos in the provider module, the method could be used, e.g. to assess seabed quality according to the Benthic Quality Index introduced by Rosenberg et al. (2004).

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